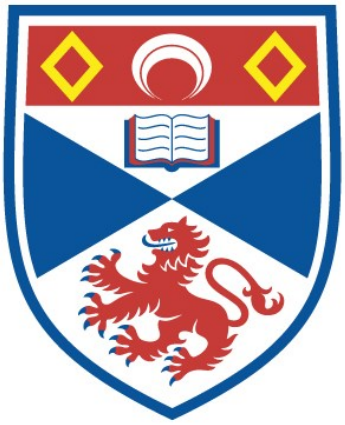
BEHAVIOUR, ECOLOGY AND RECRUITMENT OF IMMATURE GUILLEMOTS 'URIA AALGE'

Duncan Halley

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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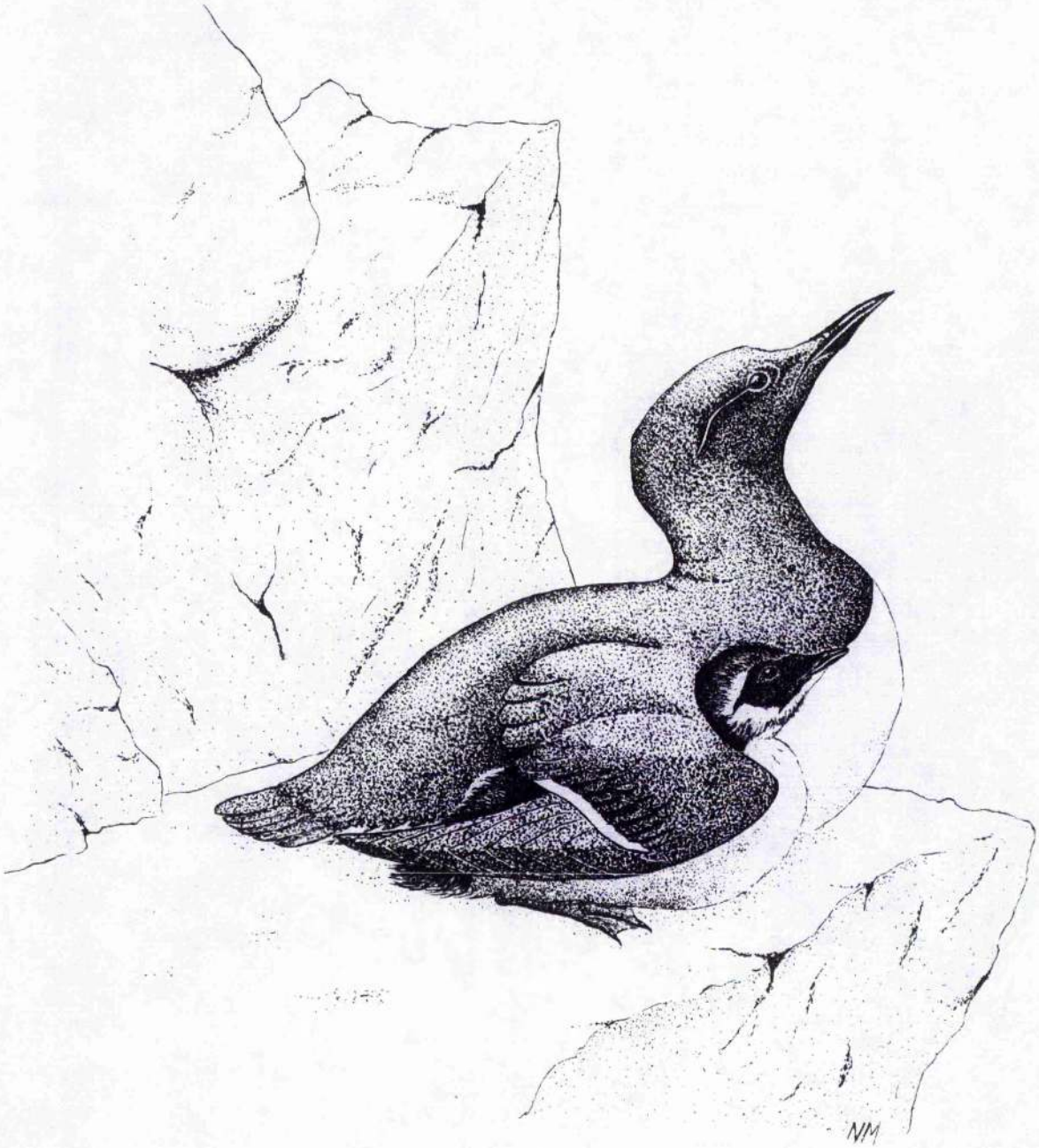
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I, Duncan John Halley, hereby certify that this thesis has been composed by myself, that it is a record of my own work, and that it has not been accepted in partial or complete fulfilment of any other degree or professional qualification.

Signed Date: 27/9/92

I was admitted to the Faculty of Science of the University of St. Andrews under Ordinance General No. 12 in October 1987 and as a candidate for the degree of Ph.D. in September 1988.

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Abstract

Guillemots have been studied on the Isle of May since 1980. Between 184 and 581 individually identifiable birds were ringed as chicks each year since 1983. Cumulative known survival rates varied from 14-39% for cohorts at least 3 years of age. Survival rate was highly significantly negatively correlated with the number of hours of gale force winds in the three months after a cohort first goes to sea. Immatures did not return to the colony until at least 2 years of age. The proportion of a cohort attending the colony increased, cohorts arrived at the colony earlier in the season, and individuals were seen more often up to the age of 4-5. Experienced individuals arrived earlier, were seen more often, and were more likely to recruit than inexperienced birds of the same age. Two and 3 year olds but very few older birds visited sea rocks below the colony; all ages were seen on top ledges and on sites within the breeding colony. Immatures tended to visit the same subcolony repeatedly; older cohorts were more sedentary. Guillemots were highly philopatric to their natal subcolonies as prebreeders and recruits. Recruitment age varied from 3 years to 8+, median 6. Recruits fledged 0.26 chicks/pair compared to 0.79/pair in the breeding population as a whole. Recruits arrived earlier in the year of recruitment, and in the previous year, than same-aged birds which did not recruit. Substantial numbers of immatures from other colonies visited the Isle of May and Isle of May bred birds were observed elsewhere. Non-native immatures were seen fewer times than natives. Activity at the colony varied little between immature cohorts, but suggested increasing competitive ability with age. The results are discussed in relation to wider issues in seabird behaviour and ecology

Chapter 1

Introduction and Literature Review

This thesis examines the period of deferred maturity and recruitment in a pelagic seabird, the common guillemot *Uria aalge*. This phase of seabird life history has received considerable attention in recent years as long term studies of seabirds have revealed that it is of particular importance in understanding life history strategies and population dynamics in the group (see Wooller *et al* 1992 for review) . To understand why this should be so, it is necessary to first consider what is known of the behavioural ecology of seabirds, and in particular of the ecological and behavioural processes underlying deferred maturity.

Pelagic seabird species, though divided taxonomically into four orders, show a characteristic set of adaptations to their environment. These include low clutch size (usually one), colonial nesting, low adult annual mortality, deferred maturity, and dual parental care (Lack 1968). Neritic species show similar trends, but tend to have larger clutch sizes, smaller colonies with less rigid nest site requirements, and to begin breeding at a younger age. That this dichotomy is an adaptive response is strongly suggested by its convergent evolution in the three orders containing both pelagic and neritic species (all Procellarids are pelagic): Charadriformes (Nettleship & Birkhead 1985), Sphenisciformes (Croxall & Prince 1985; Warham 1975), and Pelecaniformes (Nelson 1978).

Several authors have looked for an ecological explanation for this complex of adaptations. Wynne-Edwards (1962) attempted to do so in terms of Group Selection, arguing that individuals restrain breeding to prevent overexploitation of resources in the interests of the population as a whole. This view suffers from

serious theoretical difficulties, in particular that a "selfish mutant" which does not restrain breeding will be favoured by natural selection, and is not generally accepted (e.g Maynard-Smith 1976). More widely accepted approaches are based on a view emphasising selection at the level of the individual, in particular that animals are selected to maximise their inclusive fitness (i.e. genetic contribution to the next generation; Maynard-Smith 1972).

Lack (1954,1966,1968) used a comparative approach to argue that the dominant feature shaping the behaviour and ecology of birds in general was density dependent competition for food. In pelagic seabirds, population levels are regulated through winter mortality due to starvation, especially of juveniles. In the breeding season, the increase in food supply is such that it is not a limiting factor. Deferred maturity is a result of the need to acquire sufficient foraging competence to be able to reproduce successfully. In addition, deferral of breeding may reduce mortality risk; in long-lived species this will be advantageous if it increases the chances of surviving to breed better in subsequent years thereby increasing lifetime reproductive success (see below). Lack noted that a reduction in reproductive output in this way might conceivably limit populations, but considered that the narrower "bottleneck" (as it later became known) for population numbers remained density-dependent winter mortality. This could play a part in producing deferred maturity if younger birds emerge from the winter in a condition so poor that they have insufficient reserves to allow them to breed. Recently, some correlative evidence for a link between weather conditions, plankton and herring abundance, and the timing of breeding and breeding success of kittiwakes which is consistent with this hypothesis (Aebischer *et al* 1990) has been found. However, in Lack's view, the breeding adaptations shown by pelagic seabirds, including deferred maturity, result largely from density independent difficulties in obtaining food during the breeding season, and not through density-dependent competition, which operates outside the breeding season only.

Ashmole (1963,1971) disagreed. In tropical seas there are relatively few islands on which seabirds can breed, and in his view the concentration of birds at the breeding colonies puts far greater pressure on surrounding food supplies than on the resources of the much larger nonbreeding range. Density dependent competition for food therefore results, acting mainly through egg and chick mortality, and through the inability of less experienced birds to attain breeding condition. Deferred maturity arises directly out of the main population limiting parameter and is a direct response to ecological factors rather than experience *per se*. Relative, rather than absolute foraging competence (as Lack implied) is the determining factor in preventing young birds from breeding. Several studies have shown a decline in age of first breeding where adult mortality increases or the food supply is superabundant (see below).

Ashmole applied his theory specifically to the relatively aseasonal climates of tropical oceans, and believed that it might not apply to colder climates with marked seasonal variations in food availability and a generally greater availability of safe breeding locations. Whether this is the case will depend both on the degree of breeding concentration and the level of increase in food availability. Furness & Birkhead (1984) and Birkhead & Furness (1985) noted that in the North Sea sizes of colonies of gannet *Sula bassana*, shag *Phalacrocorax aristotelis*, puffin *Fratercula arctica* and to a lesser degree kittiwake *Rissa tridactyla* were negatively correlated with the sizes of conspecific colonies within foraging range. Furthermore, there are negative relationships in a number of species, including common and Brünnich's guillemot *Uria lomvia*, between colony size and factors such as clutch size, breeding success and fledging weight, apparently through intraspecific competition (Gaston *et al* 1983; Birkhead & Furness 1985; Hunt *et al* 1986). Promontory colonies in Alaska, with a larger potential feeding area available, are significantly larger than linear-coast colonies (Birkhead & Furness 1985). Birt *et al* (1987) found that bays closer to double-crested cormorant *Phalacrocorax auritus* colonies had

much lower benthic fish populations late in the summer than those further away, although crustacean assemblages in all bays were similar and large numbers of fry were found in rocky refugia in the depleted bays. Cormorants fed c16km from the colony at this time, close to their foraging limit, clearly suggesting prey depletion and competition for food. Several other studies also suggest, indirectly, that competition for food supplies around the colony is considerable. Baird (1991) found that nonbreeding tufted puffins *Lunda cirrhata* ate more pelagic prey than breeders, which fed mainly on neritic species. Breeding birds were restricted to inshore waters by the time and distance constraints inherent in brooding and provisioning eggs and chicks. Similarly, Klomp (1990) demonstrated that the size of immature great skua *Catharacta skua* clubs reflected food availability around the colony. Wiens & Scott (1975) calculated that seabirds consume 22% of inshore fish production off Oregon. Bailey & Hislop (1978) calculated that 5-10% of sprat and sandeel annual yield in the N. sea is consumed by seabirds, while Furness (1978) calculated that 29% of the annual fish production within 45km of Foula was consumed by seabirds. Ford et al (1982) estimated that a 10% reduction in food supply off St. George Island, Alaska, would adversely affect reproductive output, and a 40% reduction lead to complete reproductive failure. Croxall & Prince (1980) considered that the greatest pressure on food supplies around S. Georgia occurred during the breeding season. However, Gales & Green (1990) found for little penguins *Eudyptula minor* that, although adult consumption of food was very high in the chick rearing period (in excess of 60% of body weight/day) birds did not lose condition. In winter, when energetic demands were much less, but nevertheless in excess of energy intake, birds lost weight and condition and mortality was highest. This population was able to rear supernormal broods of three, and so food supply in the breeding season does not appear to be a limiting factor. Similarly, Williams (1991) found that winter foraging trips were longer, subsequent breeding numbers were lower (-20%), average breeding dates later, and recruitment much reduced in gentoo penguins *Pygoscelis papua* after a winter in which the preferred prey, krill,

was scarce in the diet in the midwinter months. Conversely, in the following winter and breeding season, krill remained the dominant food throughout, foraging trips were shorter, breeding began over a month earlier and the breeding population greatly increased (+84%). Breeding success per pair, and adult weights during breeding, did not vary between years, suggesting that winter food supplies and not summer levels were primarily affecting breeding numbers and perhaps timing. Taken together these results suggest that, while not a general rule, density-dependent competition for food does occur during the breeding season in some populations outwith the tropics, and consequently that Ashmole's mechanism for deferred maturity may operate.

Theoretical treatments investigating deferred maturity in particular, rather than as part of a general theory of adaptation, all emphasise life history evolution and the role of tradeoffs between mortality risks and breeding proficiency as the pressure producing deferred maturity (see Partridge & Harvey 1986 for a review). That such tradeoffs can occur in seabirds has been shown by Stonehouse (1960): adult King penguins *Aptenodytes patagonius* which reared chicks were found to have higher mortality rates than those which failed to do so. Sibly & Calow (1986) demonstrated that, in the absence of tradeoffs, delayed reproduction is never advantageous except under certain stringent conditions which rarely if ever occur in the wild. Stearns & Crandall (1981) identified four possible tradeoff mechanisms which might select for deferred maturity : a) a gain in fecundity, b) an improvement in offspring survival, c) increased fitness of offspring in years of catastrophic juvenile mortality, and d) as a general product of K-selection (MacArthur and Wilson 1967) for an environment dominated by intraspecific competition. Curio(1988) found for organisms that provision and/or protect their offspring that a single measure, the ratio of the mean number of breeding attempts to the maximum number, successfully predicted the length of deferred maturity in species as diverse as eggplant lace bug *Gargaphia solani*, great tit *Parus major*, and Californian gull

Larus californicus. The higher the adult survival rate, the larger this ratio tends to be. The underlying mechanism, by implication, is that the gain from reproductive restraint per future breeding episode need be proportionately smaller in longer lived species for deferred maturity to be favoured. Moreover, Wittenberger (1979) demonstrated that this effect was reinforced where breeding risk relative to output was especially high for subadults, as appears to be commonly the case in seabirds (see below). The potential power of this mechanism was demonstrated by Goodman (1974). Given a population demography typical of a pelagic seabird, reproductive effort will only be selected for if the fractional amount by which fledging success increases is at least 19 times greater than the fractional amount by which parental survival is decreased. The precise demography of individual species will affect this result somewhat, however it indicates the potential effect on life history evolution of relatively small increases with age in foraging, competitive, and/or reproductive skills.

The r/K selection theory (MacArthur & Wilson 1967), and by implication Lack (1968) and Ashmole (1963,1971), contend that delayed maturity is one consequence of a predictable environment in which individuals are primarily competing with conspecifics for resources. However, Schaffer (1974) has shown that variation in fecundity due to an irregularly fluctuating environment may also select for reduced reproductive effort in all individuals if this enhances personal survival. This allows the individual to hedge bets against a succession of poor years. Unfortunately, it is difficult to tell in most temperate ocean seabirds whether resource fluctuations are natural or caused by man and therefore only of recent occurrence in evolutionary terms. Deferred maturity is strongly selected for under this schema if the resource fluctuations affect younger age groups more severely. There is a considerable body of evidence to support this assumption (see below).

To summarise, theories of seabird adaptation emphasise the role of foraging ability in the production of deferred maturity; the balance of current evidence favours the view that younger birds are unable to gain sufficient food in competition with more experienced and efficient older birds to reproduce successfully. Theoretical treatments of life history evolution postulate a tradeoff between reproductive output and mortality risk. Where an organism improves its efficiency at feeding over time, so that the mortality risks associated with reproduction lessen, it will be selected to avoid reproduction while young if to do so means that, on average, it will then produce more offspring which themselves survive to breed in the course of its lifetime than it would if it bred immediately. Where the species is long lived, as in most seabirds, the immediate gains in reproductive output must be very large in relation to the increased risk of mortality for reproduction to be favoured. There is some theoretical evidence that, given a long lifespan, deferred maturity is favoured (for different reasons) in both stable and irregularly fluctuating resource environments.

A general assumption of explanations of deferred maturity (except that of Wynne-Edwards) is that young birds are deficient, either in absolute terms or when in competition with adults, in their ability to forage for food. This places them at a disadvantage in the ability to produce, or cost of production of, viable offspring. Lack inferred this from the generally higher mortality and lower weights of immature birds and there has since been much direct evidence (see Burger (1990) for a review). Jansen (1990) found that silvereye *Zosterops lateralis* (a small passerine) foraging efficiency improved progressively reaching adult levels at three years. No one year old birds attempted to breed, but c. 50% of second year birds, and almost all older birds, did so. Similarly, American avocets *Avosetta americana* take two years to reach adult levels of foraging efficiency and never attempt breeding at one year old (Burger & Gochfeld 1986). Several studies of neritic seabirds confirm this pattern e.g glaucous-winged gull *Larus glaucescens* (Searcy

1978), herring gull *Larus argentatus* (Greig et al 1983), olivaceous cormorant *Phalacrocorax olivaceus* (Morrison et al 1978), brown pelican *Pelecanus occidentalis* (Orians 1969), and sandwich tern *Sterna sandvicensis* (Dunn 1972). Foraging efficiency in pelagic seabirds is difficult to study; however, Kirkham (1980) found that the regurgitations of immature gannets were smaller than those of adults and concluded they fed less well. More refined analyses have shown that foraging proficiency improves progressively with age, in herring gulls reaching adult levels in the year before first breeding (Greig et al 1983). Initial deficits are greater for more difficult foraging methods (as measured by the interval between each catch in adults) (Burger 1990). In a study of Bonaparte's *Larus philadelphia*, ring-billed *Larus delawarensis* and herring gulls, adult proficiency was reached in the spring prior to first breeding. Importantly, the species with longer periods of deferred maturity began with relatively greater performance deficits than those with shorter periods (MacLean 1986). Success in kleptoparasitic attacks in particular improves with age in gulls (Schell et al 1983; Carroll & Cramer 1985).

Other factors may influence the length of deferred maturity; for example, there is often a sex difference in average age of first breeding, though there is no evidence of sex differences in foraging ability. Females typically begin reproduction earlier than males (Burger 1990), though in the kittiwake the reverse is true (Aebischer & Coulson 1990). This may be due to factors such as differential mortality, resulting in more experienced mates being available for one sex (see also below), as appears to be the case in kittiwakes, to sex differences in parental investment, and/or to sex differences in the energetic requirements for breeding. It is clear, however, that foraging ability is an important constraint on the potential ability of a young bird to satisfy the heightened energetic demands of breeding, and that foraging efficiency improves with age over the first few years of life.

A major early cost of a breeding attempt for females is the formation of an egg or clutch. In many species, including the guillemot, the female departs to sea for a period of from a few days to over a month after insemination, apparently to gather resources for egg formation. Unlike other early costs, such as nest site and mate acquisition, the size and quality of egg produced, and the subsequent fate of hatchlings, are easily monitored and there are a number of studies, although few have been able to separate the effects of age and experience. Egg size has been found to increase with parental age/experience over the first few breeding seasons in the herring gull (Davis 1975), kittiwake (Thomas 1983), gannet (Nelson 1966), razorbill *Alca torda* (Lloyd 1976) and fulmar *Fulmarus glacialis* (Weimerskirch 1990) and with body condition in the lesser black-backed gull (Houston et al 1983). Kittiwakes breeding for the first time also lay fewer eggs (Coulson & White 1958; Coulson 1972). Larger eggs have been shown to produce larger hatchlings and a higher fledging rate. In the hooded crow *Corvus corone cornix*, hatchling weight and size are highly correlated with egg size, as is the size of the residual yolk sac (Rofstad & Sandvik 1987); larger eggs have a higher hatching success in wandering albatrosses (Croxall *et al* 1992). Snow goose *Anser caeurulescens* goslings from larger eggs survive post-hatching starvation better (Ankney 1980) and large lapwing eggs give rise to heavier chicks with higher survival rates (Galbraith 1988). Egg and chick weights are closely correlated in the puffin, common and Brünnich's guillemots, and razorbill (Birkhead & Nettleship 1984); heavy Brünnich's guillemot hatchlings both grow more rapidly and go to sea heavier than lighter hatchlings (Birkhead & Nettleship 1982), though whether this enhances post-fledging survival rates is not known; Harris *et al (in press)* found no effect of chick condition on postfledging survival in common guillemots. Switching experiments in herring gulls have shown that smaller eggs produce less viable chicks even when position in clutch and parental quality are taken into account. In the kittiwake, egg weight is correlated with fledging success independent of female age (Thomas 1983).

In the guillemot, Hatchwell & Pellatt (1990) found that favourable feeding conditions, inferred from high colony prelaying attendance, resulted in an earlier average laying date, a shorter period of yolk deposition, and a higher proportion of albumen, lipid, and non-lipid solids within the egg. Egg dimensions and composition were significantly correlated between years for the same females; Hatchwell & Pellatt (1990) considered that this was due to variations in female genetic quality, but female age was not taken into consideration and may have contributed to the observed results. Croxall *et al* (1992) were able to separate the effects of age and experience in their long-term study of wandering albatrosses *Diomedea exulans* : age, but not breeding experience, significantly affected egg size, older birds laying larger eggs; hatching success was enhanced with higher age/experience, but the effect was not significant for either separately. Perrins (1970) noted that, in general, birds which lay later in the season have a lower breeding success (though in one population of fulmar late layers were found to be more successful (Hatch 1990)). This implies a selection pressure for earlier laying and that late laying birds are constrained from breeding earlier. Hatchwell (1991) found that early-laying guillemots which had their first egg removed showed no reduction in fledging success with their replacement egg if breeding synchrony on a ledge was maintained, and their success remained higher than that of naturally late-laying birds, suggesting a difference in intrinsic quality between birds. Harris *et al* (*in press*) showed that, in some years, late fledging birds had lower survival rates, although whether this was related to parental quality or to fledging date as such was not known.

Younger birds also appear to have greater difficulty in chick rearing, and incur greater costs—specifically higher annual adult mortality—in the course of a breeding episode (see Ryder 1980 for an overview). In both fulmar and antarctic fulmar *Fulmarus glacialoides*, inexperienced pairs fed young less frequently and fledged fewer offspring (Ollason & Dunnet 1986; Weimerskirsch 1990). Similar

results have been found in gannets (Nelson 1966) and kittiwakes (Coulson 1960), though both Nelson and Weimerskirsch emphasise deficiencies in parental care rather than feeding ability as a cause of low success in inexperienced birds (but see Kirkham 1980 for gannets). Hatch (1990) has shown that inexperienced pairs of fulmars breed disproportionately badly when breeding success in general is poor. One possible reason for the prevalence of poor success in early breeding attempts is the necessity for young birds to test their breeding abilities by producing a clutch and gauging their abilities and deficiencies (Curio 1983). Evidence on this point is scant; however, in the yellow-eyed penguin *Megadyptes antipodes*, birds which first bred at two years old showed a typical reduced level of breeding success. Those which bred first at three years were as successful as adult birds and same age birds that had bred previously (Richdale 1957), contrary to expectations if Curio's (1983) hypothesis was correct.

Both the lesser quality of eggs and reduced provisioning of nestlings by first time breeders may reflect reproductive *re*straint, rather than reproductive *con*straint (Curio 1983). Given that young birds may avoid breeding in order to enhance lifetime fitness (see above), birds at the point where pressures to breed and to defer breeding are closely balanced may be selected to attempt to breed, but to make a lower investment. This results in reduced success, as observed, but nonetheless represents the optimal path for a bird at that stage in its life history. In following years, the balance of the tradeoff between reproduction and survival tilts still further and birds reproduce normally. Since both reproductive restraint and constraint produce identical results they are difficult in practice to separate.

Age also affects colony attendance and site holding. Colony attendance often commences several breeding seasons after fledging—at about 2 years old in gannets (Nelson 1966,1978); 2-3 in auks (Swann & Ramsay 1983; Hudson 1985) and kittiwake (Porter 1988); and 5-7 in the wandering albatross (Pickering 1988). In

succeeding years, the bird returns to the colony earlier in the season and leaves later and the duration and frequency of individual visits tend to increase in those species studied: kittiwake (Porter 1988), wandering albatross (Pickering 1988), pigeon guillemot *Cepphus columba* (Nelson 1987) and razorbill (Lloyd & Perrins 1977). Behaviour at the colony also changes with age and/or experience, the two often being difficult to separate. In the guillemot, there is a shift in attendance from "clubs", usually on tidal rocks, to top ledges above breeding sites or to the breeding colony (both on breeding sites and on positions unsuitable for breeding) (Birkhead & Hudson 1977; Harris *pers comm; pers. obs.*). In kittiwakes, attendance at a particular site increased with experience of the colony (Porter 1988); in wandering albatrosses male nest site tenacity, and the tendency of both sexes to be paired, increases with experience (Pickering 1988). This pattern of behaviour may reflect increasing foraging efficiency, permitting both longer attendance at the colony and energy expenditure on prereproductive behaviours, or an increased effort on such activities as the threshold of recruitment approaches. The two factors may work together, and are in practice doubtfully separable.

Studies following the recruitment of individuals of known age are providing insights into the complexity of recruitment behavioral ecology. Most of the information available originates from a long term study by Coulson and others of a kittiwake colony in NE England. Birds at this colony bred on the window ledges of a warehouse, providing a unique degree of accessibility (Coulson & Thomas 1985).

Both age and previous colony experience appear to play a role in recruitment. Recruiting kittiwakes have always been present in at least one breeding season beforehand, but birds never recruit until at least three years old (Porter 1988). These birds temporarily appropriate adult sites, often with chicks, while adults are absent (Monnat *et al* 1990). Compared with same aged birds, birds which recruited

the *following* year arrived earlier, stayed later and spent a greater proportion of the time at the colony (Porter 1988). In apparent contrast, wandering albatrosses which were to recruit the following year left the colony much earlier than other same age birds (Pickering 1988), but in that species pairing has been completed by that stage and nest site defence is unnecessary. When kittiwakes returned to recruit, they arrived later than same age birds which were experienced breeders but earlier than same aged birds which did not attempt breeding (Porter 1988). Experienced breeders laid earlier than same age recruits (Coulson & White 1958). Whether these results arise from a greater investment on the part of recruiting versus nonrecruiting birds, or because they are more efficient foragers, is not clear. That the latter is at least partly the case is indicated by the heavier weight of recruits compared with same age nonrecruits (Porter & Coulson 1987); this finding may also indicate that competition for breeding sites is a factor in recruitment, since weight and fighting ability are usually highly correlated (Krebs & Davies 1984). Quality of site and/or mate also influences recruitment. Average age and weight of recruitment declined both when additional nest sites in the core of the colony (see below) were provided, and when adult mortality rose (Porter & Coulson 1987). Earlier recruitment where adult numbers are depressed has been found in other seabird species (Coulson et al 1982; Williams & Joanen 1974; Duncan 1978). Male kittiwakes tend to recruit when younger than females (Aebischer & Coulson 1990); this may be related to the higher adult mortality among males, decreasing the competition for experienced mates and/or quality sites. Similar results have been found in other gulls (Mills 1973).

Recruits also segregate by "quality" in kittiwakes. Birds in the core part of the colony both survived better (despite higher levels of agonistic interaction) and bred more successfully than birds nesting at the periphery (Coulson 1968; Aebischer & Coulson 1990). This was despite any apparent differences in nest site quality (as is the case in shags, Potts 1980) and in the absence of predation. Competition for core

sites, which tend to be more densely concentrated, may stem from an adaptation to predation avoidance, as appears to be the case in guillemots (Birkhead 1977). Alternatively, a system of conventional competition may be operating. Intrasexual competition for access to core sites (by both sexes) may indicate that successful opposite sex competitors are of high quality and therefore better mates. That central site recruits are of higher quality, rather than greater experience, is strongly suggested by the finding that they are *younger* on average than recruits to peripheral sites. Older birds which did manage to recruit to the centre had a poorer reproductive performannce than the younger recruits (Wooller & Coulson 1977). Centrality has also been shown to be positively correlated with breeding output in Adelie penguins *Pygoscelis adeliae* (Tenaza 1971). In some guillemot and puffin populations, breeding success is positively correlated with nesting density (Birkhead 1977; Harris 1980). Porter (1990) described three patterns of individual recruitment in kittiwakes. Early returnees gained central sites, replacing dead or partner changing mates of experienced breeders. Birds arriving later either took peripheral sites or delayed several weeks and attempted to establish new sites in the centre. Of the later arrivals, birds attempting to establish in the centre were heavier (and therefore probably better competitors) than those recruiting to the periphery. However, they risked not being able to establish in time to breed at all that year, and if they did, did so late and with a lower success. The compensating factor was presumably greater reproductive success in later breeding seasons.

To summarise, theoretical treatments of both seabird biology and deferred maturity point to the crucial role of foraging efficiency as the ultimate cause of delayed breeding. In the last twenty years research results have generally confirmed this view. Much evidence now exists showing that young birds are deficient in foraging ability compared with adults, and apparently initially more so in species where maturity is longer deferred. In addition, younger birds may be selected to invest less in reproduction than older birds. Mechanisms through which foraging

deficiency and/or reproductive restraint may affect breeding have been investigated: egg size and efficiency in provisioning young appear to be important factors. The precise age of first breeding appears to be affected by social factors such as the availability of experienced mates and high quality sites. Recent work (mainly on kittiwakes) on the behaviour of recruiting seabirds has revealed a complex process involving several alternative stategies. These presumably involve their own tradeoffs of cost and benefit for birds of varying competitive ability.

Knowledge of variations in the timing, numbers, and patterns of recruitment can have profound effects on the understanding of population structure and dynamics in the population as a whole (Chabryzk & Coulson 1976). Where, as in seabirds in general and guillemots in particular, the recruitment system is complex, simple models of resource change are unlikely to produce accurate predictions of population response. Complex systems, albeit based ultimately on simple inputs, tend to be driven in part by the nature or "rules" of system interactions, (as in red grouse, Watson *et al* 1984), and may at first sight appear to show little relation to ecological conditions. For example, conditions in the Isle of May guillemot colony appeared generally optimal in the period 1981-86; breeding success and adult survival rates were high but fewer young returned to the colony than expected. This was thought to be the major cause of a levelling off in numbers of the colony after a period of rapid increase. The factors causing the poor recruitment were unknown (Harris & Wanless 1988). An improved understanding of the process of recruitment in guillemots is clearly key to a more complete understanding of the population dynamics of the species.

This thesis approaches these problems by examining the behaviour of individually identifiable immature and recruiting guillemots of known age at the colony on the Isle of May, Scotland. Chapter 2 describes the study population and general fieldwork methods. Chapter 3 considers the return and survival rates of immatures

in relation to ecological variables and populations. Chapter 4 examines patterns of attendance at the colony and Chapter 5 the distribution of immatures within the colony. Chapter 6 deals with recruitment into the breeding population and initial breeding success. Chapter 7 describes evidence of intercolony movements in immature guillemots and its implications for population dynamics in the species. Chapter 8 investigates the social, site-ownership and agonistic activity of immatures while attending the colony. Chapter 9 reviews the findings of the study in relation to other seabirds and to the broader pattern of guillemot adaptation, and suggests areas for further research.

Chapter 2

Study area and Methods

2.1 The Isle of May

The Isle of May (56°11'N 2°33'W) is situated on the western edge of the North Sea in the mouth of the Firth of Forth, Scotland (Figure 2.1), 8km SSE of the Fife shore and 14km NNE from the Lothian shore. The island is 57ha. in area, c.2km along the long axis (NW-SE), and c.500m at the widest point (Figure 2.2). It is formed of a sloping volcanic sill of olivine-dolerite (greenstone) terminating on the west in steep cliffs and stacks rising directly from the sea to up to 50m. From these the island slopes north eastwards to a low rocky shore with offshore rock outcrops and small (<10m) wave-cut cliffs. At high tide two islets at the northern extremity of the island and a number of smaller rocks are separated from the main mass. Fault lines running roughly east-west have been eroded to form gullies and, in the largest, low inland cliffs.

From earliest records the seabird colony on the island has been its most prominent feature. The name May itself derives from the Norse *Maeyar*, meaning gull or seabird (Sturlusson 1225). The North American term for guillemots, murre, probably derives from the same root. Studies of the birds and other wildlife of the island began in the early part of the 20th century (Baxter & Rintoul 1918), and a bird observatory was established in 1934 which, with an interruption due to Naval occupation of the island during the second world war, has been operational ever since. In 1956 the island became a National Nature Reserve and in 1989 was purchased by the Nature Conservancy Council for its scientific and conservational

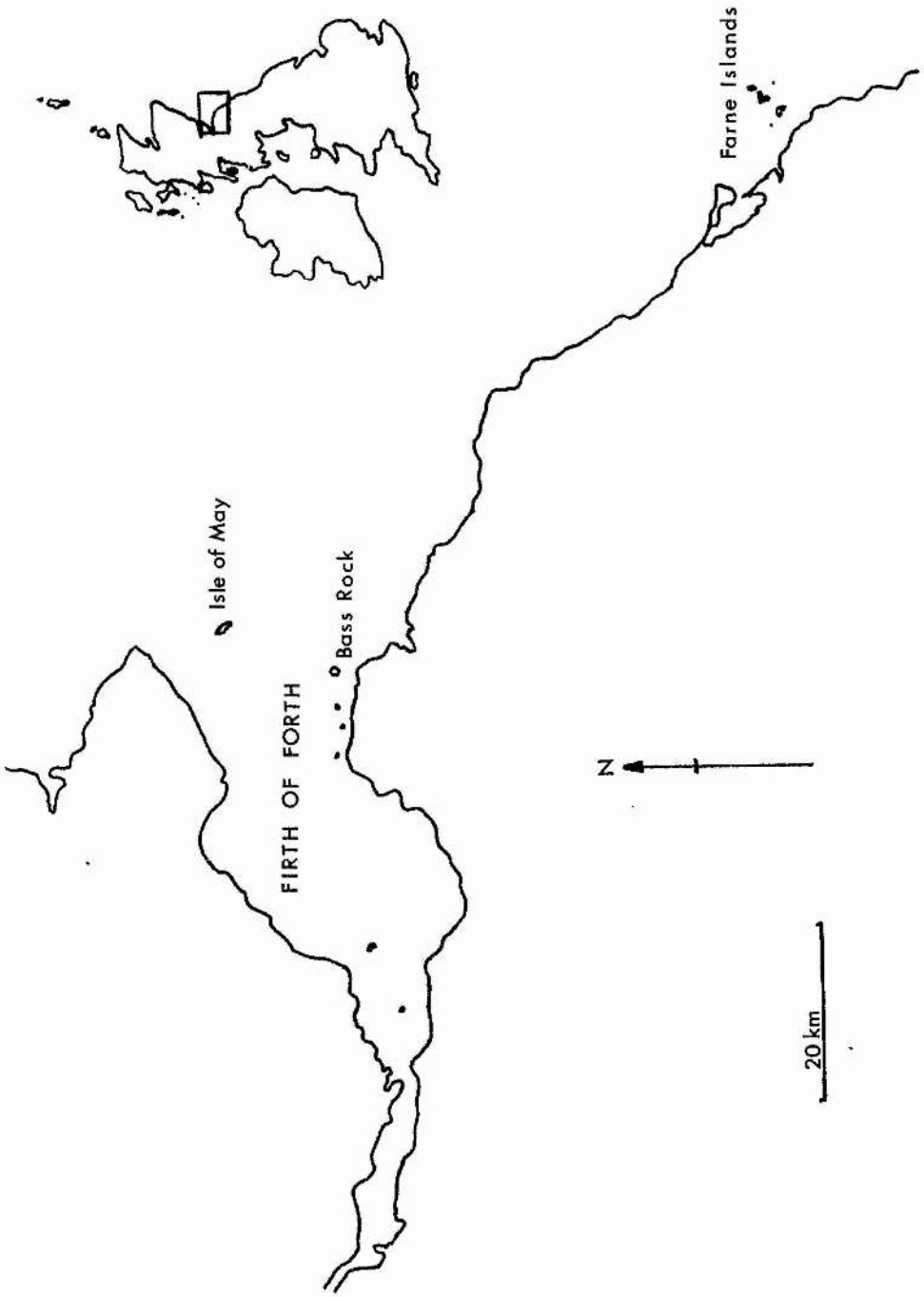
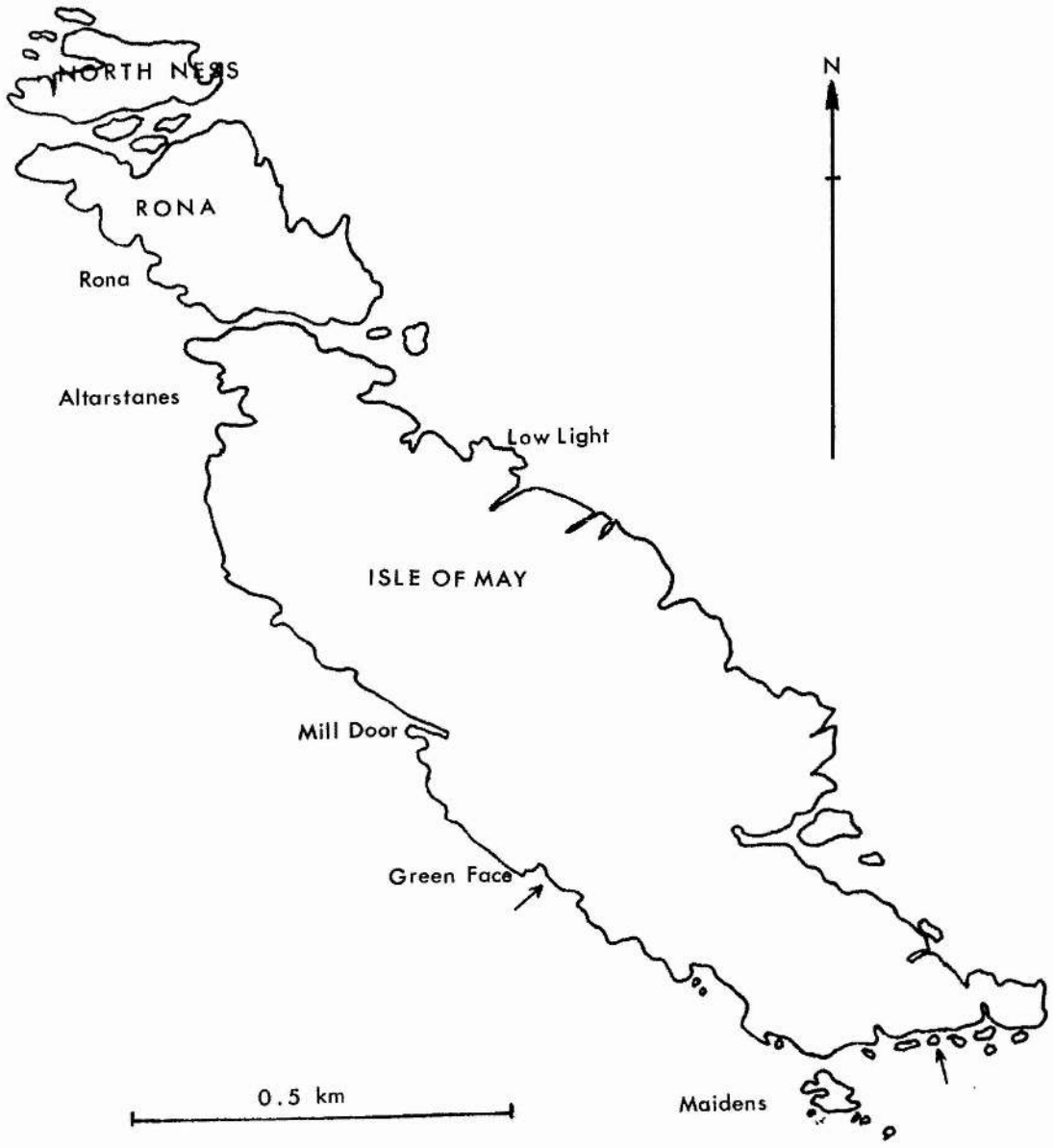


Figure 2.1: Location of the Isle of May

Inset : position of main map in relation to the British Isles

Figure 2.2: The Isle of May. Locations of subcolonies mentioned in the text that are outside the focal area of the colony are shown. Arrows indicate the limits of the focal area of the colony (see Figure 2.3)



importance. Eggeling (1974) describes the island's history, vegetation and animal life.

The Isle of May is a major seabird station, holding important breeding populations of shag, kittiwake, puffin, razorbill and guillemot, large colonies of herring and lesser black-backed gulls *Larus fuscus*, and fulmars (Harris & Galbraith 1983). Recently, common *Sterna hiundo* and arctic *Sterna paradisaea* terns have re-established after a long absence. 2-3 breeding pairs of great black-backed gulls *Larus marinus* are the only regular predators of adult seabirds on the island.

2.2 The guillemot colony

The guillemot colony on the Isle of May is long established (Eggeling 1974). Marking and detailed scientific study of the population by M.P. Harris, S. Wanless, and others commenced in 1980.

In common with many other seabird species on the island, and in the North Sea generally (Harris 1990), the guillemot population increased from the early 1970s, roughly doubling in numbers up to the early 1980s, and then declined slightly (Harris & Galbraith 1983, Harris 1990; Figure 2.3). In 1990, 16778 birds or 12632 pairs were counted; in 1991 16834 birds or 11440 pairs (Harris *pers comm*; Harris *et al* 1983 for census techniques).

Ringing of chicks commenced in 1981; adult mortality and mean productivity of young up to the time they left the colony varied little throughout this period (Table 2.1). Adults did appear to have to expend greater effort in provisioning young in later years, although this trend was reversed in 1988-89. The decline in population observed was tentatively attributed to poor levels of return (and so presumably survival) and recruitment of immature birds (Harris & Wanless 1988; Harris 1990).

Figure 2.3: The Isle of May guillemot population, 1972-1991

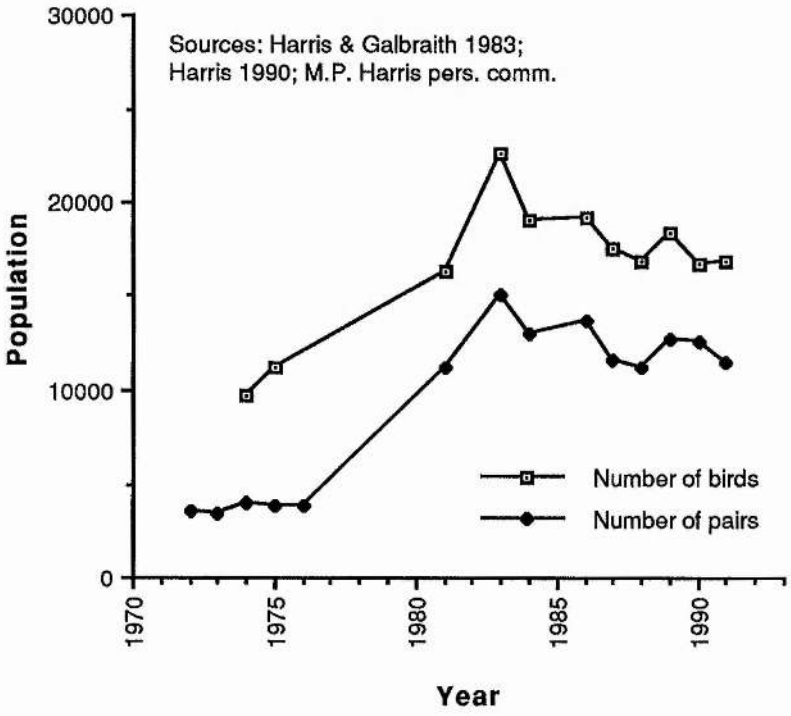


Table 2.1: Selected breeding and survival measures of Isle of May guillemots.

Source: Harris (1990; *pers. comm.*)

Parameter	Year										
	81	82	83	84	85	86	87	88	89	90	91
Median laying date (May)	8	8	7	5	7	10	8	6	3	8	?
Young fledged/ pair laying[a]	.81	.79	.77	.73	.80	.82	.76	.85	.85	.78	.81
Leaving weight (g)[b]	?	249	250	262	262	264	252	252	254	247	261
Adult survival[c] (%)	?	93	93	93	94	97	93	92	95	91	?

[a] Mean of 5 study plots except for 1981 (2), 1982 (4) and 1983 (4).

[b] Leaving weight is the mean weight of chicks with wing lengths of > 60mm.

[c] Overwinter between year n and year n+1.

2.3 Fieldwork Methods: Terminology

2.3.1 Subcolonies

Guillemots breed mainly on the west side of the island, on cliffs, stacks, and rocky areas nearer sea level. For the purposes of research, the colony has been divided into a number of subcolonies. A subcolony is a section of cliff, not including the tidal rocks below, on which guillemots breed, including unoccupied sites and top ledges above the area occupied by breeding birds. The boundaries of subcolonies are usually semi-natural, often areas of cliff on which guillemots do not breed or promontaries separating approach flight lines, but can be arbitrary. They are, however, consistent. In one case (Dense and White Ledge), two areas regarded as separate subcolonies occupied the same cliff frontage but are separated vertically by a cliff face on which there are no birds. Locations of subcolonies are given in Figs. 2.2 & 2.4.

2.3.2 Clubs

Clubs are concentrations of subadults and (in other species) nonbreeding adults at the colony, usually in peripheral parts of the breeding areas. They occur in many seabirds, e.g Sulids (Nelson 1979), and skuas (Davis 1976). Under some definitions, top ledge concentrations of subadults (see below) could be classified as clubs, but I have chosen to separate them for two reasons. First, Birkhead and Hudson (1977) and Hudson (1979) defined guillemot clubs as concentrations of subadults on tidal rocks and to apply the same term more widely could cause confusion. Second, sea rock clubs and top ledges may be demographically and functionally separable. The latter provide potential for observing adult behaviour and assessing breeding opportunities as well as the social interactions available at sea rock clubs, and the birds are, on average, older than those on sea rocks. In

Figure 2.4: Subcolonies in the focal area of the colony

1. Lady's Bed
2. South Horn
3. Chatterstanes
4. The Angel
5. Colony B
6. South of South Face
7. South Face
8. Colony Four
9. Stack
10. White Ledge
11. Dense
12. Hide Face
13. Cornerstone

addition, top ledge concentrations are found only where suitable nonbreeding sites and ledges are not available among the breeding birds (Chapter 6); otherwise, subadults are usually mixed in with breeding pairs. This suggests that they are at least partly different in function to sea rock clubs. Clubs are therefore defined as concentrations of subadult birds on tidal rocks or areas directly accessible (i.e. without flying) from tidal rocks. On the Isle of May, clubs varied from large, regularly occupied areas to small, irregularly occupied niches containing only a few birds. Locations of the principal clubs in the focal area of the colony are shown in Figure 2.5.

2.3.3 Top ledges

On vertical cliffs immatures usually concentrate on ledges above the breeding birds at the top of the cliff (Chapter 6). In recent years some birds have begun to breed in these areas, presumably because sites lower down are not available. Top ledges are defined as areas above the main breeding ledges occupied primarily by immature birds.

2.3.4 Types of breeding ledge

A **site** is a general term for a ledge, part of ledge, or niche apparently sufficient for one pair of guillemots to breed on, whether or not it was so used.

Single sites are small rock platforms or niches suitable for a single pair only. Groups of birds breeding on single sites would be classified as "sparse" in Birkhead's (1977) classification.

Ledges are narrow shelves of cliff containing two or more actual or potential sites distributed along the ledge. Sites could be bounded on up to two sides by other

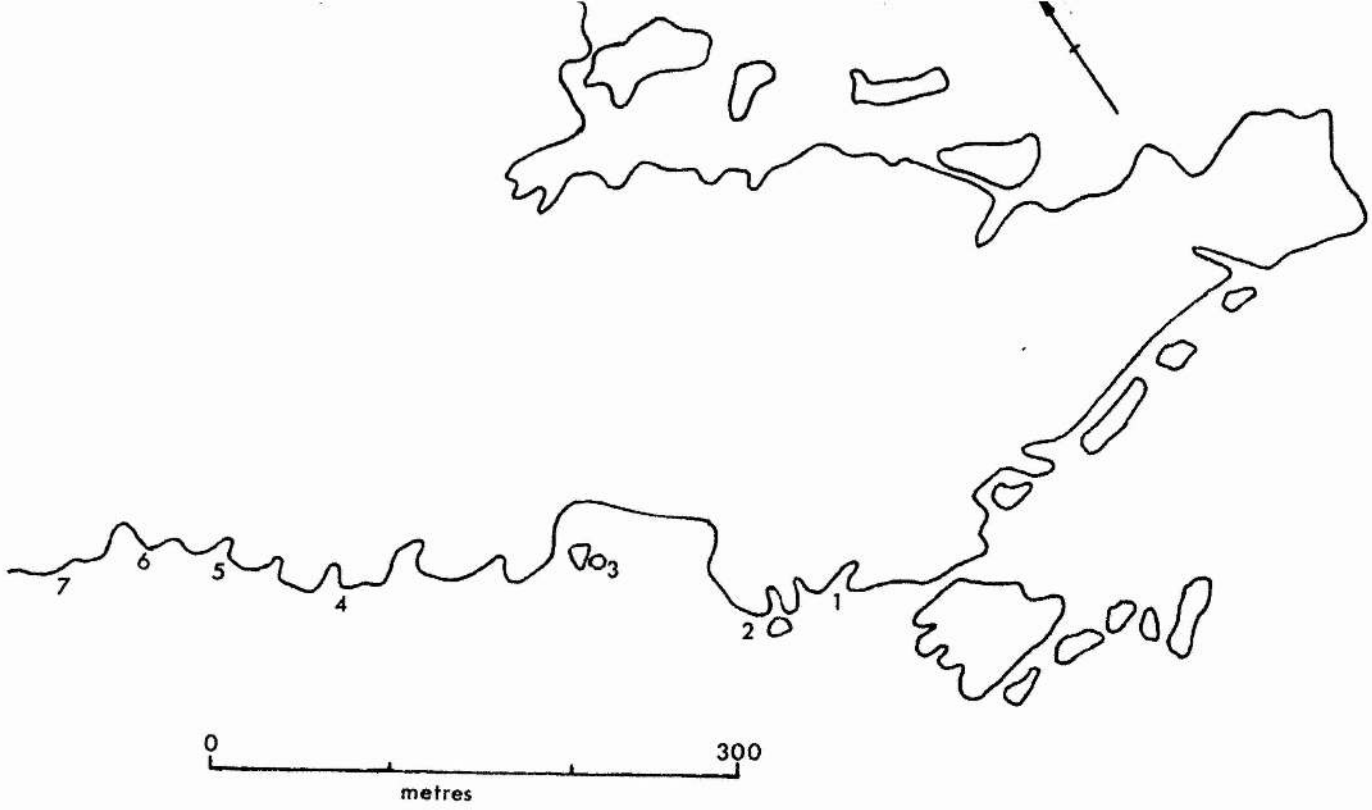


Figure 2.5: Principal clubs in the focal area of the colony. Smaller tidal rock ledges and boulders throughout the focal area were also used as club sites

1. South Horn sea rocks

2: Chatterstanes sea rocks

3: Pilgrim stack

4: South Face sea rocks

5: Dense sea rocks

6: Hide sea rocks

7: Green Face sea rocks

sites; the third side cliff face and the fourth by the cliff edge. This is medium density according to Birkhead's (1977) classification.

Broad ledges are ledges or stack tops wide enough to hold sites more than one site deep, so that sites could be bounded on all sides by other sites. In these areas guillemots typically breed in body contact with conspecifics at densities of >10 pairs/m^2. Broad ledge birds bred at "Dense" concentrations according to Birkhead's (1977) classification.

Birkhead (1977) noted sparsely populated broad ledges in his declining Skomer study colony. On the Isle of May, if an area was occupied at all, it was always occupied to close to the maximum density the topography permitted so that sparsely populated broad ledges, for example, did not occur. The use of previously unoccupied top ledge sites for breeding suggests that breeding sites were in short supply during the study period.

2.3.5 Half-sites and toe-holds

Half sites are locations where a guillemot can stand but which are too small or sloping to breed on.

Toe holds are cracks or the edges of ledges (or broad ledges) to which birds can cling but not fully settle.

A schematic representation illustrating this classification of colony topography is given in Figure 2.6.

Figure 2.6 : Schematic diagram of guillemot colony illustrating classification given in text

A: Club

B: Broad ledge

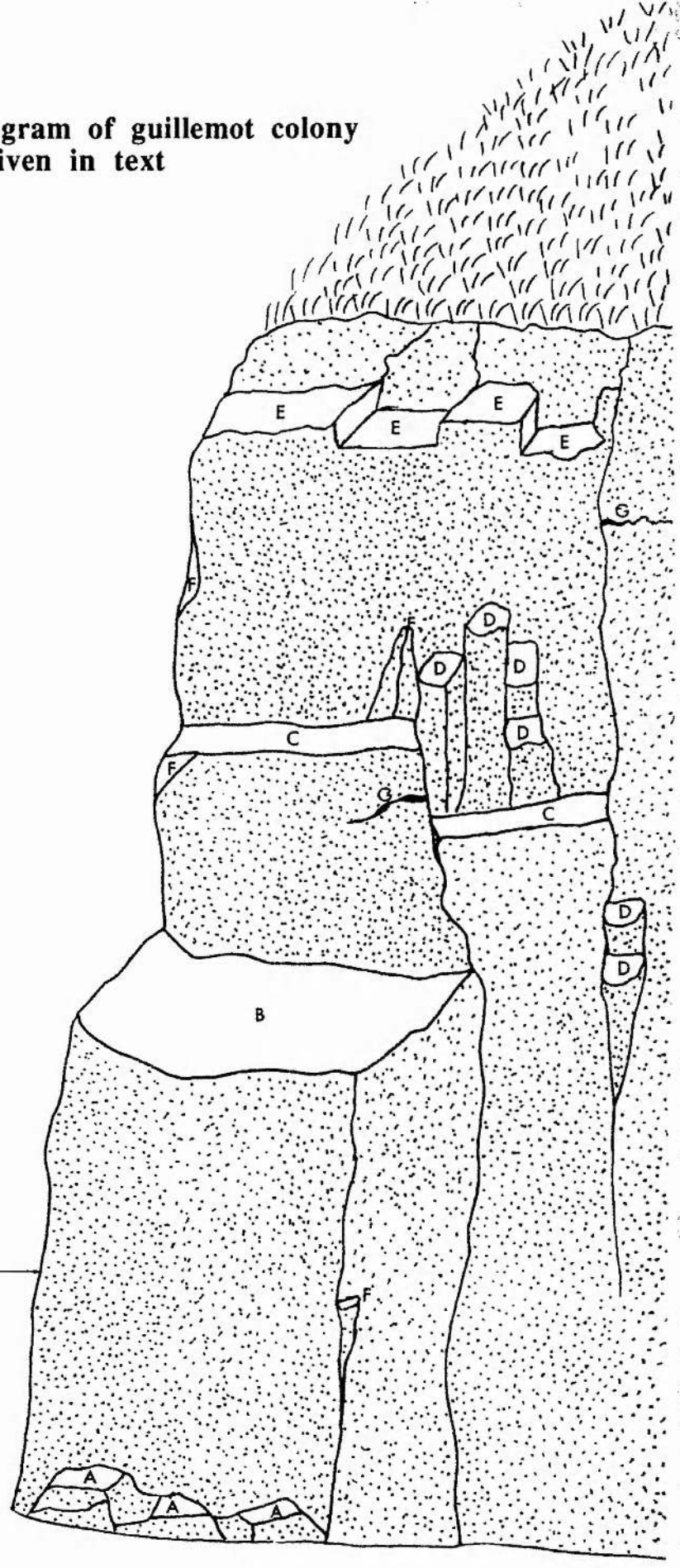
C: Ledge

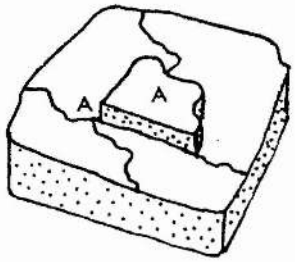
D: Single site

E: Top ledge

F: Half site

G: Toe hold. Birds also use the extreme edges of ledges as toe-holds.





2.3.6: Population classification.

The population of guillemots was classified into several groups based on the stage reached in their life history and current breeding status as follows:

An **Immature** was a bird which was not known to have previously bred and did not breed during the current breeding season.

Recruits were birds breeding or attempting to breed for the first time. The criterion for a breeding attempt was that the bird was a member of a pair which laid an egg.

Nonbreeders were birds of unknown previous status which did not breed in the current breeding season.

Former breeders were birds which had bred in previous seasons but did not do so in the current breeding season.

Adults were breeding birds which had previously bred or attempted to breed.

2.4 General Fieldwork Methods

This section describes the ringed population on which most of the study is based and provides an outline of the general survey methods by which the attendance and location of birds was noted. Specific fieldwork techniques and methods of analysis are dealt with in the appropriate chapters.

2.4.1 Ringing

A few guillemots were ringed as pulli in 1981 and 1982; systematic ringing with BTO metal rings (bearing unique serial numbers) and cohort colour rings began in 1983. From 1988 some of the colour rings were engraved with a unique 1-3 digit number. The numbers ringed in each year were variable (Table 2.2). Early in the study, standard circular BTO wrap-around metal rings were used. On land, guillemots walk on their lower tarsi. This meant that part of the number was always obscured and, over time, the inscription would be worn away. From mid 1983 these were replaced with special guillemot rings (Figure 2.7) which display the number upright on both sides of the leg. This improves readability greatly and almost eliminates wear on the inscription. With practice such rings could be read easily with 10x binoculars or a 15-45x telescope at ranges up to 60m in good light. It was normally possible to approach birds much more closely.

A large number of adults, mainly on South Face, Colony Four, Hide Face and White Ledge were ringed with a BTO numbered metal ring and three colour rings. The combination of these rings was unique to each bird so that each was readily identifiable. In the present study, these birds constituted a control group against which the behaviour of immatures could be measured.

In each year as part of the general ringing effort some apparent nonbreeders of unknown age and origin are caught and given full colour combinations; in 1990 and 1991 more of these birds were caught (46 in 1990, 29 in 1991) and given combinations incorporating a special green-and-white ring indicating their status as nonbreeders and probable immatures. Most of these birds were caught on White Ledge.

Table 2.2: Numbers of chicks ringed on the Isle of May, 1983-89.

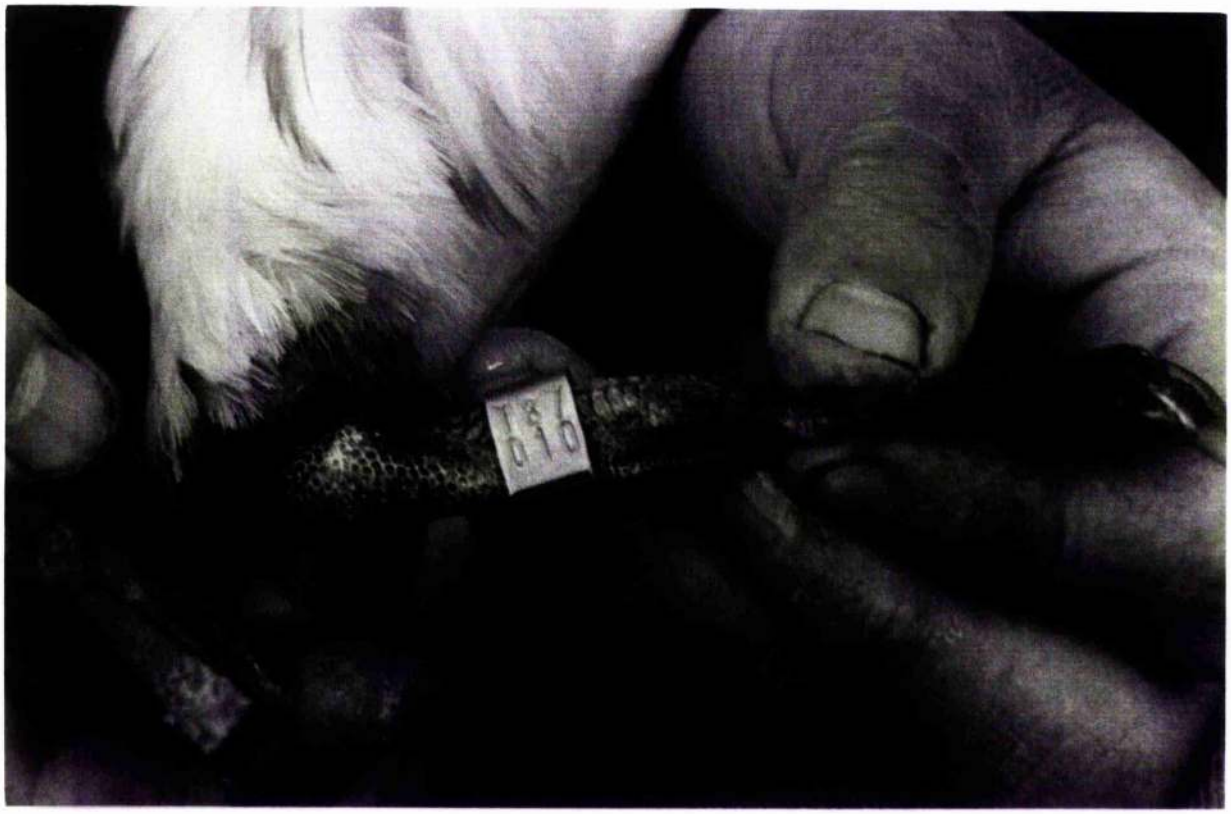
Cohort	Colour ring	Total ringed	BTO[a]+ plain colour ring	BTO + engraved[b] colour ring	BTO ring only
1983	Yellow	194[c]	133	0	61
1984	Lime	267	249	0	18
1985	White	184	171	0	13
1986	Blue	256	248	0	8
1987	Orange	243	219	0	24
1988	Green	370	67	194	109
1989	Red	581	0	306	275

[a] See Figure 1

[b] Colour rings engraved with a 1-3 digit number in a contrasting colour. Each number unique for that ring colour.

[c] 68 old-style and 126 special guillemot BTO rings (Figure 1) were used (see text). Of these 52 birds with old style rings and 81 with guillemot specials also had yellow colour rings attached. New style rings were used in all subsequent years.

Figure 2.7 British Trust for Ornithology Guillemot ring. The serial number is presented upright on both sides of the leg.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016

2.4.2 Fieldwork dates

Fieldwork began in October 1989 and ended in July 1991, covering two complete breeding seasons. M.P. Harris and S. Wanless earlier recorded much information invaluable to this study, particularly on immatures seen in previous seasons. The colony was visited for a minimum of eight days each month from January-March, with the exception of December when sustained high winds prevented landing (Table 2.3). In the winter of 1990-91 birds were apparently absent until late February: there were very few birds in October (M.P. Harris *pers comm*), no sign of recent droppings on the cliffs during a visit in January, and no return of birds to the mainland colony at St. Abb's Head (40km SE) until late February (K. Rideout, *pers comm*). Birds were present on the Isle of May in large numbers by 15 March (*pers. obs*).

The main field season commenced on 30th April in 1990 and 13th April in 1991. Fieldwork ended on 20th July in 1990 and 22nd July in 1991, three and two days respectively after the last immatures were seen that season. Absences from the island during the main field season are given in Table 2.4.

2.4.3 Colony monitoring

Population levels were monitored each year by M.P. Harris and others using methods described in Harris *et al* (1983). Figures given below were supplied by M.P. Harris (*pers. comm.*) except where otherwise noted.

Birds were observed using 10x40B Zeiss Dialyt binoculars, or a 15-45x60 Bushnell Spacemaster telescope. At a minimum, the date, time (GMT) and location for each bird was recorded each time it was seen and later transferred to a card index. Coverage of the colony was divisible into four categories:

Table 2.3: Summary of winter fieldwork dates 1989-90

Month	Arrival Date	Departure Date	No. days fieldwork
October	14th	27th	13
November	15th	24th	9
December	-	-	-
January	6th	16th	10
February	14th	23rd	9
March	23rd	31st	8

Arrival and departure dates varied as landing on the island is dependent on calm weather conditions. Prolonged bad weather prevented landing in December.

Guillemots were apparently absent from the Isle of May in whe 1990-91 winter until later February (see text). Preliminary fieldwork for the 1991 breeding season was carried out 13th-16th March.

Table 2.4: Breeding season fieldwork dates

Season	From	To	Breaks in fieldwork
1990	28/4	20/7	17/5 - 20/5 29/5 - 4/6 20/6 - 21/6
1991	13/4	22/7	4/5 - 7/5 31/5 - 3/6 25/6 - 26/6

1) Not covered. This applied to the Maidens subcolony only, sited on rocks cut off from the main island except at low tide, and then not accessible without causing disturbance to the birds. The subcolony was visited once or twice in each year to ring pulli, but there were no opportunities to search for visiting immatures. Occasionally, cohort-ringed birds were seen from the main island, but were too distant for ring numbers to be read. In both years the subcolony contained 200 pairs of guillemots, about 2% of the total population.

2) Irregularly covered. This category applied to the high cliffs between Green Face and Altarstanes, excluding the low rocks at Mill Door (Figure 2.2). These subcolonies were very large, containing 8643 and 7346 pairs (68% and 64% of the total) in 1990 and 1991 respectively. Birds were not ringed on these cliffs, and vantage points from which to view them were fairly distant. Searches of these cliffs for ringed birds were conducted fairly frequently, but not to any schedule, and coverage of the area had a low priority.

3) Nonsystematically covered. The outlying broken rock subcolonies fell into this category: Mill Door, Rona, and Low Light (Figure 2.2). These contained 634 and 733 pairs (5% and 6% of the total) in 1990 and 1991 respectively. An attempt was made to visit these subcolonies as often as possible, and they were visited on most days. The timing of visits was not regular, however. Pulli were ringed at all these subcolonies.

4) Focal subcolonies. These were subcolonies between Lady's Bed and Hide Face inclusive (Figure 2.3). Almost all of the adult and nonbreeding birds ringed were ringed here, as well as many pulli. This area comprised c.600m of coast containing 3155 and 3161 pairs of guillemots (25% and 28% of the total) in 1990 and 1991 respectively. Fieldwork here was carried out on a regular and systematic schedule. Two censuses counting all unringed birds on immature ledges and club sites,

presumably immatures, and ringed definite immatures, were made each day, commencing at 0600 and 1700 GMT respectively. Each check took two to three hours to complete. Once each week in the 1991 season, sweeps were made along the focal subcolonies at three hourly intervals throughout the day. From 6 June these were at 0300, 0600, 0900, 1200, 1500, and 1800. Earlier in the season, the 0300 sweep was omitted as it was dark. Wind direction and speed (Beaufort Scale), cloud cover (eighths), light conditions (four-point scale), sea conditions (six point scale) and precipitation were recorded at the start of each sweep.

2.4.4 Adult attendance

Numbers of adults (and immatures) at two subcolonies, South Face and Colony Four, were counted at 0700, 1300 and 1900 each day.

2.4.5 Recruitment and breeding biology

Measures of breeding success in adults were obtained from contemporaneous studies by M.P. Harris & S. Wanless. Recruits were identified during searches of the colony and the nests checked daily thereafter.

2.4.6 Behavioural sampling

Five minute samples of the behaviour of immatures, and adults as a control group, were taken on an opportunistic basis. 513 samples were taken in 1990 and 415 in 1991. Data were recorded on an Epson HX20 portable microcomputer using a specially written BASIC programme (Appendix 1). The sample recorded the location and identity of the bird, its proximity to other birds, and the occurrence and duration of all behaviours. The initiator, other individual, and where appropriate winner, of all sexual and agonistic interactions were recorded. The resulting

information was transferred to an ORACLE database using a translation programme (Appendix 2). Statistical analyses were made from the resulting database files.

2.5 Data management and statistical methods

Ringing records and ecological data from the continuing guillemot project were stored as paper records and computer files. In 1989 I set up an ORACLE database containing most of this data.

Data collected 1989-91 for the present study was in the first instance stored on paper or index cards. Summary data was extracted from these for use in statistical analyses. Analysis was carried out using the packages MINITAB and SPSS, supplemented by computer programs taken from Cohen and Holliday (1982) (for the Jonckeere Trends Test) or written with the assistance of A. Adhikerana (Multiple Comparisons posthoc for the Kruskal-Wallis one-way analysis of variance: Appendix 3). Sokahl & Rohlf (1981), Siegel (1956), and Siegel & Castellan (1989) were the primary statistical texts consulted.

Behavioural data recorded on the EPSON HX-20 was recorded on microcassettes, transferred to ASCII files, and translated via the IBM VAX computer at ITE Merlewood into the guillemot project ORACLE database. Statistics were performed on data derived from the database using SQLPLUS command programmes.

Unless otherwise stated, tests were two-tailed and the threshold of significance was taken to be the 0.05 level. Tests were said to approach significance if they were significant at the 0.1 level.

Statistical abbreviations used hereafter are n.s. (not significant), d.f. (degrees of freedom), S.D. (standard deviation), S.E. (standard error), p (probability), and n (sample size).

Chapter Three

Ring loss, ringing recoveries and survival rates

3.1 Introduction

Population studies require accurate information on the survival rate of the population and of the individual cohorts of which it is composed. In guillemots, survival rates of adults are usually fairly easy to obtain. Individuals return to the same area each year and mortality can be measured by checking on the return of marked individuals to their breeding sites each year (e.g. Birkhead & Hudson 1977; Harris & Wanless 1988). Immatures are much more difficult to study. They are less tied to a specific area, may not visit the colony for part or all of the season, or emigrate. In the absence of individually identifiable birds of known age, previous studies have estimated survival rates from the maximum number of birds of a known age (but not individually identifiable) seen at the colony in one day (Birkhead & Hudson 1977), derived them mathematically assuming that population changes not accounted for by adult mortality are due to changes in survival rate of immatures from that colony (Hatchwell & Birkhead 1991), or argued that changes in the levels of known mortality (from birds recovered dead) may indicate changes in survival rate between cohorts (Swann *et al* 1989; Harris & Bailey 1992). The population of known-age immatures which are the basis of this study offer an opportunity to measure survival rates more directly than previously, and to test the assumption that ringing recovery rates are indicative of overall survival rates.

Once survival rates have been measured, the factors which may be causing variations in post-fledging immature survival can be explored. These fall into three broad categories: pre-fledging factors, such as growth rate and fledging weight;

prey populations; and environmental factors such as ocean salinity and wind intensity. This chapter reports on return rates of immature cohorts; factors affecting their accuracy as measures of survival; the relationship between the numbers of birds found dead and survival rate; and ecological and environmental correlates of survival rate.

3.2 Methods

Birds were identified in the course of general fieldwork (Chapter 2). The condition of both metal and darvic rings, and ring loss, were noted. Those birds which lost rings during a field season were counted as lost-ring birds for statistical purposes.

Immatures could be sexed if they were observed mating, or if they were observed to be paired with a bird of known sex. It was assumed that all pairings were heterosexual and that there were no reverse mountings, as occur in some cormorants (Ortega-Ruano & Graves 1992).

The number, location and identity of Isle of May ringed immatures recovered dead from July 1982-April 1991 were obtained through the British Trust for Ornithology ringing scheme.

Data on productivity, chick provisioning, and fledging weights on the Isle of May were taken from Harris (1991). Data on fish abundance (size classes <20cm, small enough to be potential guillemot prey) were obtained from reports of the International Council for the Exploration of the Sea of commercial catch analysis using Virtual Population Analysis (VPA) and bottom trawls in the North Sea south of 56°30'N (Anonymous 1985, 1988, 1990a,b; Harris & Bailey 1992). Unfortunately, sprat populations were too low to be measurable in this period. Data

on sea surface temperature for the mid-west North Sea were obtained from M.Colebrook, Plymouth Marine Laboratory (M.P. Harris, *pers. comm.*).

The number of hours of gale force winds (Beaufort Scale Force 8+) in July—February 1983-1989 were taken from the Monthly Weather Reports (Meteorological Office, 1983-88). The recording point selected was the Forth Bridge, 55km WSW of the Isle of May. This station, at high elevation (72m a.s.l.) and isolated from other landscape features, offered the most accurate reflection available of conditions at sea (Edinburgh Meteorological Office, *pers. comm.*). On the three occasions when this station recorded a defective record (October 1985, January 1987 and December 1987), the measurement from Leith harbour lighthouse (24m a.s.l., 45km WSW of the Isle of May) was used.

3.3 Results

3.3.1 Ring Loss

Seabird rings in general, especially those used on guillemots and razorbills prior to 1982-83, were prone to loss after several years, due to a combination of abrasion and electrolysis in sea water (Coulson & White 1955; Lloyd & Perrins 1977). Guillemots and razorbills walk mainly with their tarsi horizontal, and hence on the rings. Wear was severe and the numbers on the ring soon became partly or completely illegible. The problem was so severe that special mathematical techniques were developed to allow for ring loss in the calculation of survival rates (Haldane 1955; Mead 1974).

The special guillemot metal rings used in this study (Figure 2.7) from 1983 onwards appeared to be extremely durable. The incoloy or stainless steel alloy from which they are made is robust and the form of the ring distributes stress more

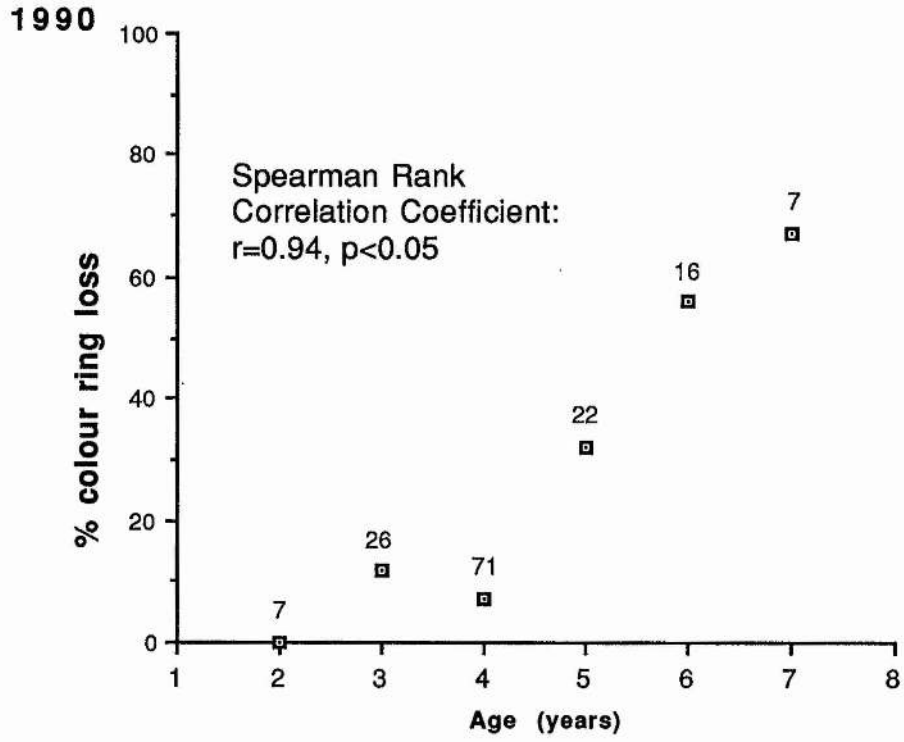
evenly across the flat base of the ring, reducing abrasion and fracturing. Nevertheless, a small number of rings were lost. The smallest chicks were not ringed, but in some borderline cases some rings probably slipped off over the ankle joint of the bird before the leg reached full size. Three birds found dead and reported by the general public, and one individual seen on the Isle of May, had colour rings only, probably as a result of the metal ring slipping off when the bird was a chick. Other rings were lost later—S. Wanless (*pers comm*) observed an adult pull the metal ring over its ankle and off when the ring was caught in a rock crevice. Nonetheless, only 1/323 birds ringed with metal and colour rings which returned to the Isle of May had lost the metal ring and not the colour ring, and partially cracked or heavily abraded rings were never seen. The rate of metal ring loss can therefore be treated as negligible.

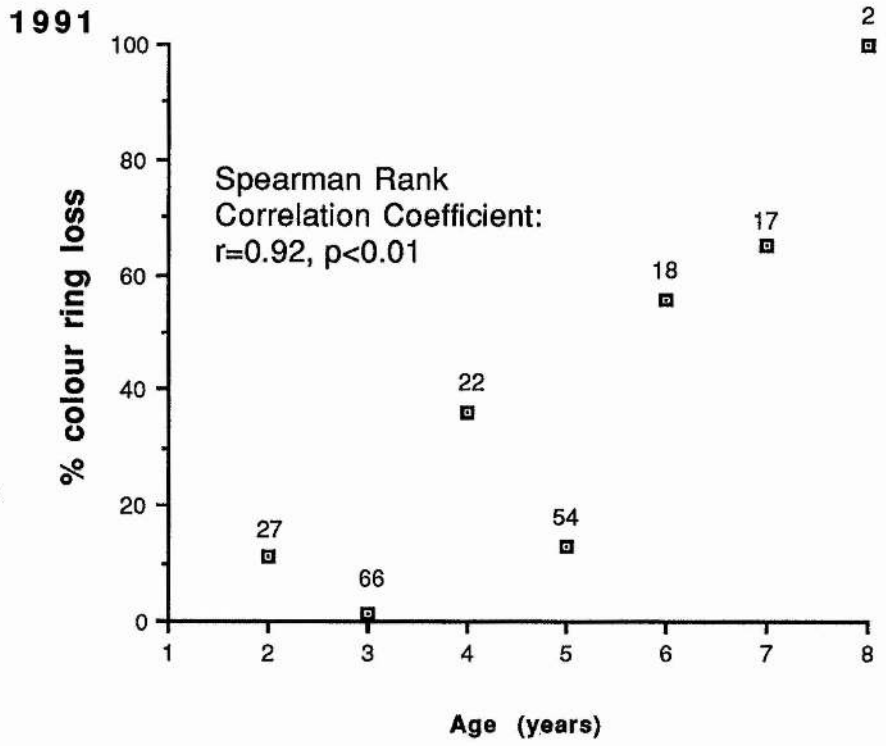
Darvic colour rings were much more likely to be lost, presumably mainly through abrasion as many rings were very thin and pieces of ring were found in the colony. There was a significant positive correlation between age and proportion of colour rings lost in both years of the study (Figure 3.1).

The loss of a colour ring may render the bird less conspicuous, so that birds without such rings would be seen less often or would be more likely to be missed altogether. Since a greater proportion of older birds have lost rings, this might introduce a systematic bias into the data.

This possibility was tested for by comparing the average number of observations of colour ringed and non colour ringed birds of the same age, assuming that the presence of a colour ring had no effect on attendance behaviour. Birds without colour rings tended to be seen less frequently; however, none of these differences were significant in either 1990 or 1991, suggesting that any differences in observability were negligible (Table 3.1).

Figure 3.1a & 3.1b: Loss of cohort colour rings in relation to age in 1990 and 1991





n=sample size

Table 3.1: The effect of colour rings on the observability of known-age immatures.

Age	No. colour ringed	No. not colour ringed[1]	Average no. observations[2]		Mann Whitney p
			ringed	not ringed	
1990					
2	7	0	1.4±0.8	-	-
3	23	3	2.7±2.5	2.0±1.7	0.51
4	66	5	5.2±6.3	3.7±2.2	0.95
5	15	7	6.8±9.6	12.3±17.1	0.59
6	7	9	2.7±1.9	1.9±2.7	0.21
7	1	5	4	7.4±10.3	-
1991					
2	25	11	2.4±2.5	1.6±1.2	0.16
3	63	2	3.9±4.3	2.0±1.4	0.49
4	16	7	11.1±11.4	5.4±4.4	0.36
5	35	10	11.1±15.3	6.6±7.1	0.77
6	2	6	30.0±39.6	13.5±19.6	0.61
7	4	7	7.8±11.6	3.7±4.1	0.92
8	0	2	-	5.5±2.1	-

[1]Birds which had lost colour rings or had never been colour ringed. Birds natal to Rona were excluded as visits there were not made systematically (Chapter 2), and most birds ringed there were not given colour rings. Immatures are philopatric to their natal subcolony (Chapter 6). A systematic bias towards observing non colour ringed birds less often would therefore result if Rona hatched birds were included.

[2] Mean ± 1 S.D.. Birds which bred were excluded from analysis.

The 1988 cohort, 3 years old in 1991, included birds marked with either engraved or plain colour rings(Table 3.1). The average number of observations did not vary between birds with engraved and plain rings (Mann-Whitney Test, z=-0.48, n.s.).

3.3.2 Recoveries

The distribution of recoveries is shown in Figure 3.2. Relatively few individuals were recovered, and most were birds in the first year of life (Table 3.2). Birds dispersed widely, recoveries being reported from northern Iceland to northern Spain. Concentrations of recoveries off the Dutch and NW German coast and in the Skaagerak/Kategaat area confirm known wintering concentrations (Mead 1974; Brown 1985). Analyses of ringing recoveries and mortality in this population have been made elsewhere (Harris 1991; Harris & Bailey 1992).

3.3.3 Recoveries and return rates

Overall recovery rates (taken as the percentage of ringed chicks reported dead when 3 years old or younger) were poorly related to subsequent return rates, and the trend was for recovery and return rates to be *positively* correlated, although a negative correlation would be expected (Figure 3.3; Spearman Rank Correlation Coefficient r_s=0.6, n=6, n.s.).

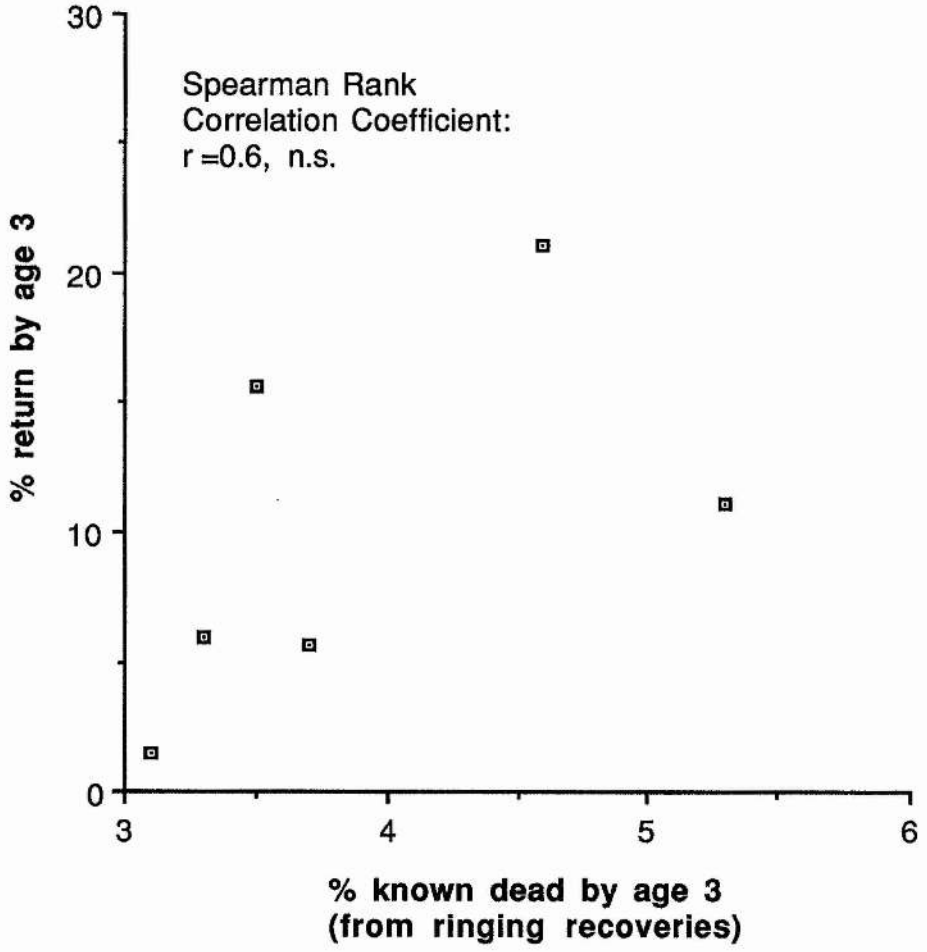
3.3.4 Return rates

Within a cohort, return rates—the proportion of birds ringed as chicks seen at the colony—increased with age from age 2 to age 4-5 (Table 3.3). No one year old guillemot has ever been seen on the Isle of May. Numbers of both the 5 and 6 year old cohorts declined in 1991 compared with the numbers of the same cohorts seen in 1990. This was thought to have been due to birds recruiting into the breeding

Natal Year	Age 1	2	3	4	5	6	7	8
1983 (n=194)	0.5	3.1	3.1	3.6	3.6	4.1	4.1	4.1
1984 (n=267)	3.0	3.4	3.7	3.7	3.7	3.7	3.7	
1985 (n=184)	2.7	3.3	3.3	3.3	3.3	3.3	-	
1986 (n=256)	0.8	3.5	3.5	5.9	6.3	-	-	
1987 (n=243)	4.1	4.9	5.3	5.3	-	-	-	
1988 (n=370)	3.8	4.6	4.6	-	-	-	-	
1989 (n=581)	2.9	3.4	-	-	-	-	-	

Table 3.2: Cumulative percentages (from ring recoveries) of known mortality of immature cohorts by a given age. Birds were classified as age 1 until the end of the first breeding season (1st August) after the breeding season in which they hatched; 2 for the subsequent year. Numbers of birds of each cohort ringed are indicated in brackets.

Figure 3.3: Relationship between return rates and known death rates in guillemots



Natal Year	Age 2	3	4	5	6	7	8
1983 (n=194)	0.5 *0.5*	1.5 *1.5*	5.2 *6.1*	5.2 *9.2*	2.6 *10.3*	4.1 *12.3*	3.6 *14.4*
1984 (n=267)	0.0 *0.0*	5.6 *5.6*	4.9 *9.4*	4.1 *10.9*	6.4 *13.5*	7.1 *15.4*	- -
1985 (n=184)	2.2 *2.2*	3.8 *5.9*	10.9 *13.0*	12.0 *19.0*	9.8 *21.7*	- -	- -
1986 (n=256)	1.6 *1.6*	14.8 *15.6*	28.1 *34.0*	21.5 *39.1*	- -	- -	- -
1987 (n=243)	0.8 *0.8*	10.7 *11.1*	9.1 *14.4*	- -	- -	- -	- -
1988 (n=370)	1.9 *1.9*	20.8 *21.1*	- -	- -	- -	- -	- -
1989 (n=581)	6.0 *6.0*	- -	- -	- -	- -	- -	- -

Table 3.3: Percentage return rates of guillemots ringed as chicks on the Isle of May. The number of birds ringed as chicks in each year are shown in brackets. Figures in normal type are percentages of guillemots ringed as chicks a given year and seen at that age. Figures in italics are cumulative percentages of all ringed chicks seen at any age, which must therefore have survived to age 2.

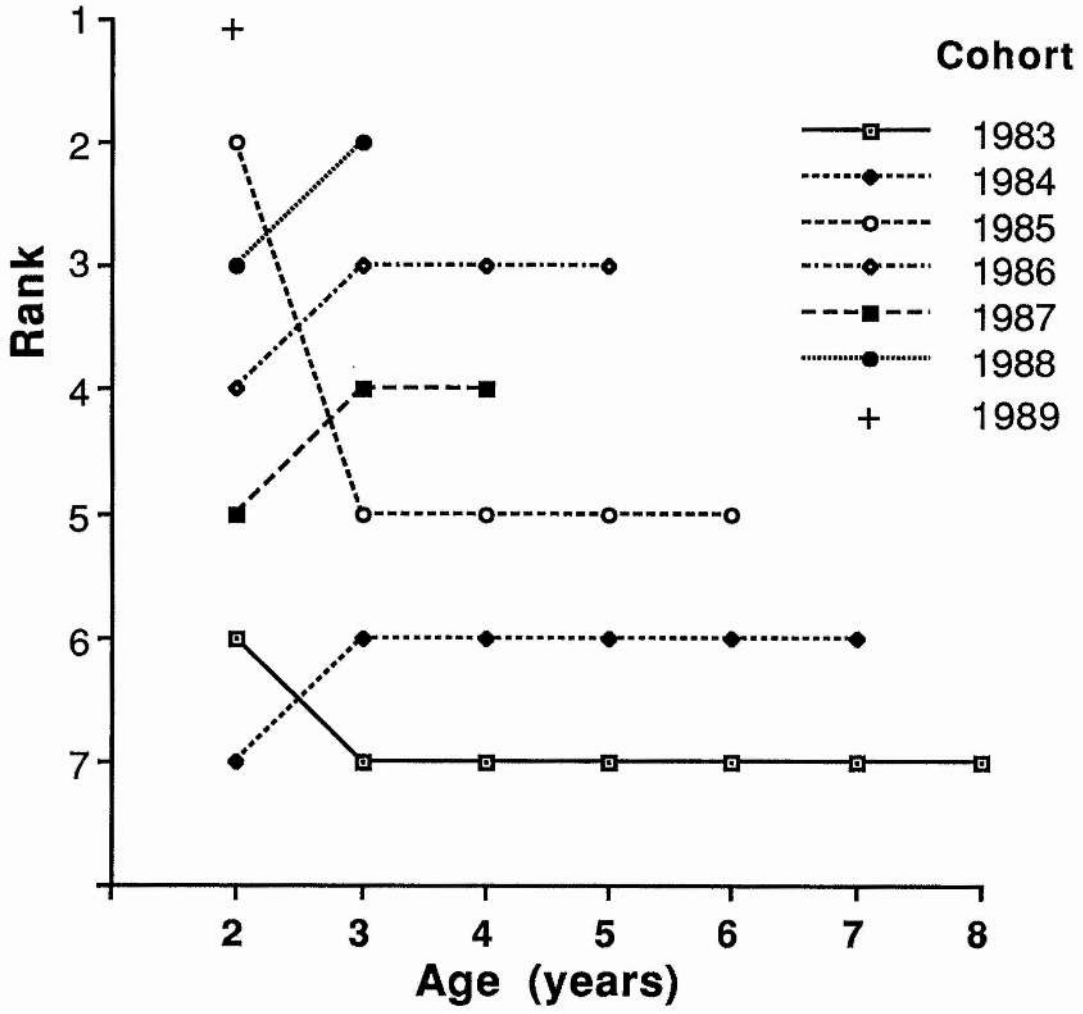
population, where they were much harder to see (Chapter 6). The cumulative return rate—all birds ever seen—continued to increase with age even in the oldest cohorts, suggesting that in all cohorts some birds which were still alive were not observed.

The age at which a bird was first seen did not vary with sex in any cohort where the sample size permitted testing (Mann-Whitney tests, n.s.); however, where all age classes were combined, a tendency for males to be seen first at earlier ages approached significance (Mann-Whitney, W=298, n_1(F)=15 n_2(M)=19, p=0.09). This may, however, reflect differences in the ease with which males and females can be sexed at younger ages rather than a real difference in the age of first return, as the younger cohorts (under 5 years old in 1991) account for most of the excess of males seen for the first time aged 2 or 3. Relatively more females may remain unsexed, although present, in the cohort at these ages.

There was considerable variation between cohorts in the proportion of birds seen at a given age (range: Age 2: 0-6%, 3: 1.5-15%; 4: 5-28%; 5: 4-21.5%; 6: 3-10%; 7: 4-7%; Table 3.2). Comparing numbers of birds seen against those not seen of the total ringed cohort, this was significant at each age except age 7 (Age 2: n.s.=43.4, 6 d.f., p<0.001; age 3: χ^2=75.8, 5 d.f., p<0.001; age 4: χ^2=86.9, 4 d.f., p<0.001; age 5: χ^2=49.6, 3 d.f., p<0.001; age 6: χ^2=8.45, 2 d.f., p<0.025; age 7: χ^2=1.8, 1 d.f., n.s.. Table 3.3). These differences were constant between cohorts (i.e the rank return rate never changed) over time after the age of 2, when relatively few birds returned (Figure 3.4). Older cohorts tended to have lower cumulative rates of return, although more years were available in which they could be observed (Table 3.3). These factors strongly suggest differential survival between cohorts early in life, assuming that emigration rates remained more or less constant.

These return rates can be compared with adult survival and breeding productivity to find whether the return rates alone were sufficient to balance mortality. Over the

Figure 3.4: Rank ordering of proportion of cohort ever seen by a given age



period 1983-88, the mean adult survival rate was 93.8±1.6% (Harris 1991). For every 100 pairs, therefore, 12.4 recruits would be needed annually to produce a stable population in the absence of immigration. Taking the productivity for each year, the percentage of fledged birds which must survive to breed to maintain a stable population can be calculated. This figure was compared with the cumulative total of ringed immatures of that cohort ever seen, and the number known to have survived to breeding age (Table 3.4). In the early years of the study, known survival lagged behind replacement level; from 1985 numbers were in excess, except for the 1987 cohort (4 years old in 1991) which was, so far, at slightly less than replacement level (but see Discussion).

3.3.5 Sex Ratios

Few known-age guillemots could be sexed with certainty. The sex ratio of birds which were sexed did not deviate significantly from 1:1 in any cohort or in all cohorts combined (Binomial Tests, $p>0.5$ n.s.; Table 3.5); however, sample sizes were small.

3.3.6 Return rate and natal year

Cohorts hatched in later years tended to have a higher return rate than earlier cohorts. The number of birds known to have returned to the island in their 2nd and/or 3rd years (see Methods) was positively correlated with year of hatching (Spearman Rank Correlation Coefficient, $r_s=0.943$, $n=6$, $p<0.01$).

Table 3.4: Levels of immature survival necessary to balance adult mortality with known survival rates of immatures on the Isle of May, 1983-88

Year	Productivity[a]	% of cohort surviving to breed to balance adult mortality[b]	% seen at any age	% seen aged 5 years+
1983	0.77	16.1	14.4	12.4
1984	0.70	17.7	15.4	10.9
1985	0.86	14.4	21.7	16.3
1986	0.81	15.3	39.1	21.5
1987	0.80	15.5	14.4	-
1988	0.86	14.4	21.1	-

[a] Data from Harris (1991)

[b] Assuming adult annual survival rate 93.8% (see text)

Table 3.5: Numbers of birds of known age and sex recorded on the Isle of May 1990-91.

Cohort	Males	Females
1983	0	0
1984	1	0
1985	3	5
1986	6	6
1987	3	2
1988	4	2
1989	2	0
Total	19	15

The sex ratio did not differ significantly from 1:1 in any cohort, or for all cohorts summed (Binomial Tests, $p>0.05$, n.s.)

3.3.7 Return rate in relation to chick feeding and growth in the pre-fledging period

Measures of chick provisioning and growth were collected on the Isle of May throughout the period in which chicks were ringed (Harris 1991). These measures included fledging weight (weight of chicks with wing length >60mm) and measures of food intake. None were significantly correlated with subsequent return rates (Figure 3.5), although the correlation between subsequent return rate and overall fledging success (no. young/pair) was quite high (r_s=0.7, n=6, n.s.; Figure 3.5).

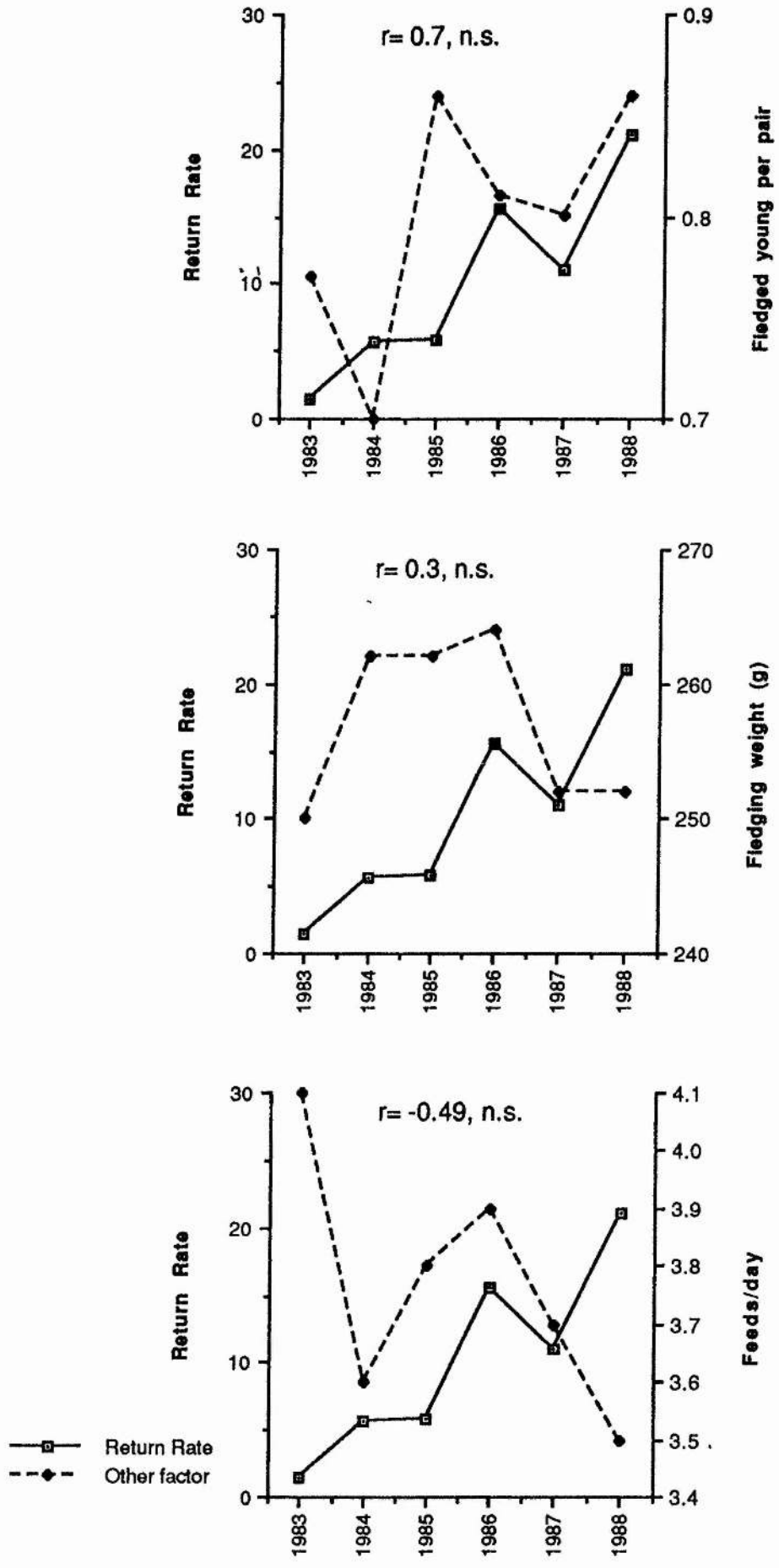
3.3.8 Return rate and prey populations

Return rate was compared with biomass of several potential prey species in the cohort's first winter of life, and of 0-group sandeels in July of the natal year. There was no significant correlation between return rate by 3 years old and any prey population measure, although the correlation with herring abundance was quite high (r_s=0.7, n=6, n.s.; Figure 3.6).

3.3.9 Return rate and environmental conditions

There was no significant correlation between sea surface temperature (as measured as deviations from the average for each three month period) in the first winter and return rate by age 3, or between gale force winds between July of the natal year and the following February (i.e. fledging-end of 1st winter at sea), measured either as hours of gales at Forth Bridge, or the number of days in which gales occurred at St. Abb's Head, Whitby and Lowestoft (Figure 3.7). During a preliminary analysis in 1990, I found a negative relationship between return rate by 3 years old and the numbers of hours of gales in July-September of the natal year. This is the period

Figure 3.5: Correlations between the percentage return rate of immatures by 3 years of age and measures of productivity, feeding levels and chick growth in the pre-fledging period. Solid lines indicate return rate, pecked lines the factor compared. The r value and significance level of a Spearman Rank Correlation Coefficient (n=6 in all cases) is shown.


r= 0.7, n.s.
Return Rate
Fledged young per pair
30
20
10
0
0.9
0.8
0.7
1983
1984
1985
1986
1987
1988
r= 0.3, n.s.
Return Rate
Fledging weight (g)
270
260
250
240
r= -0.49, n.s.
Return Rate
Feeds/day
4.1
4.0
3.9
3.8
3.7
3.6
3.5
3.4
Return Rate
Other factor

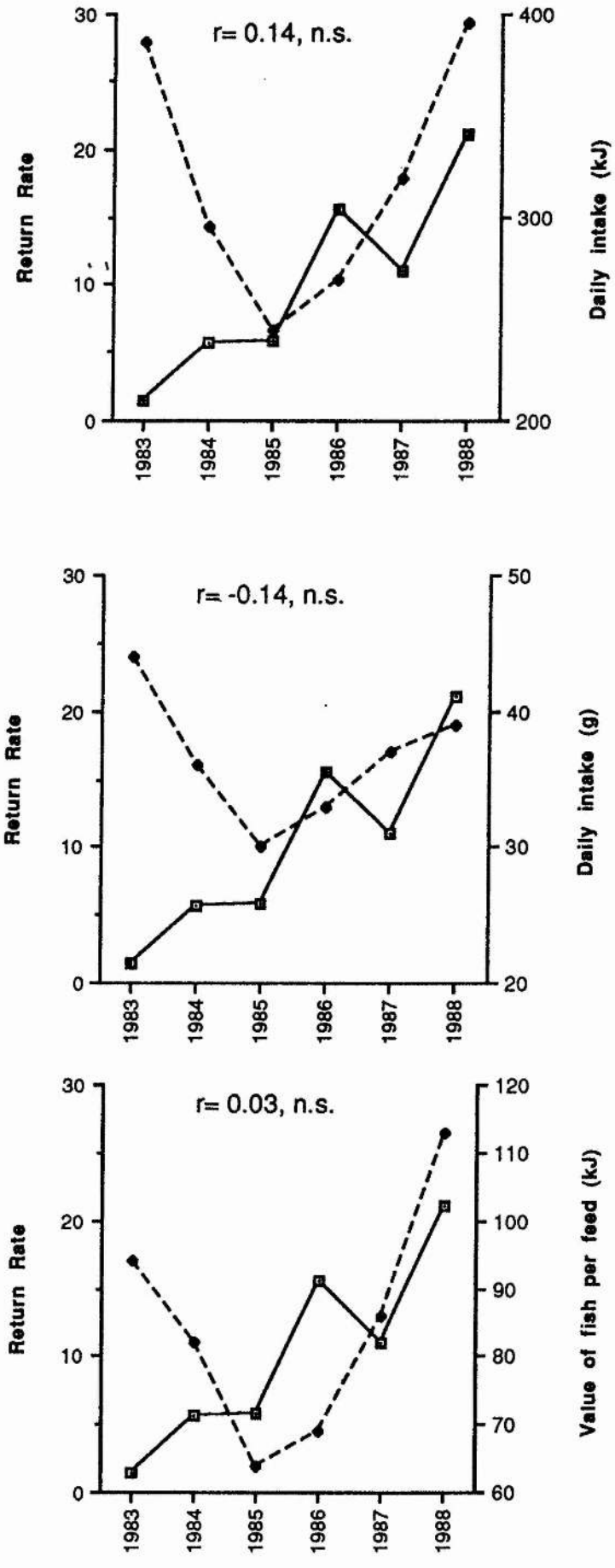
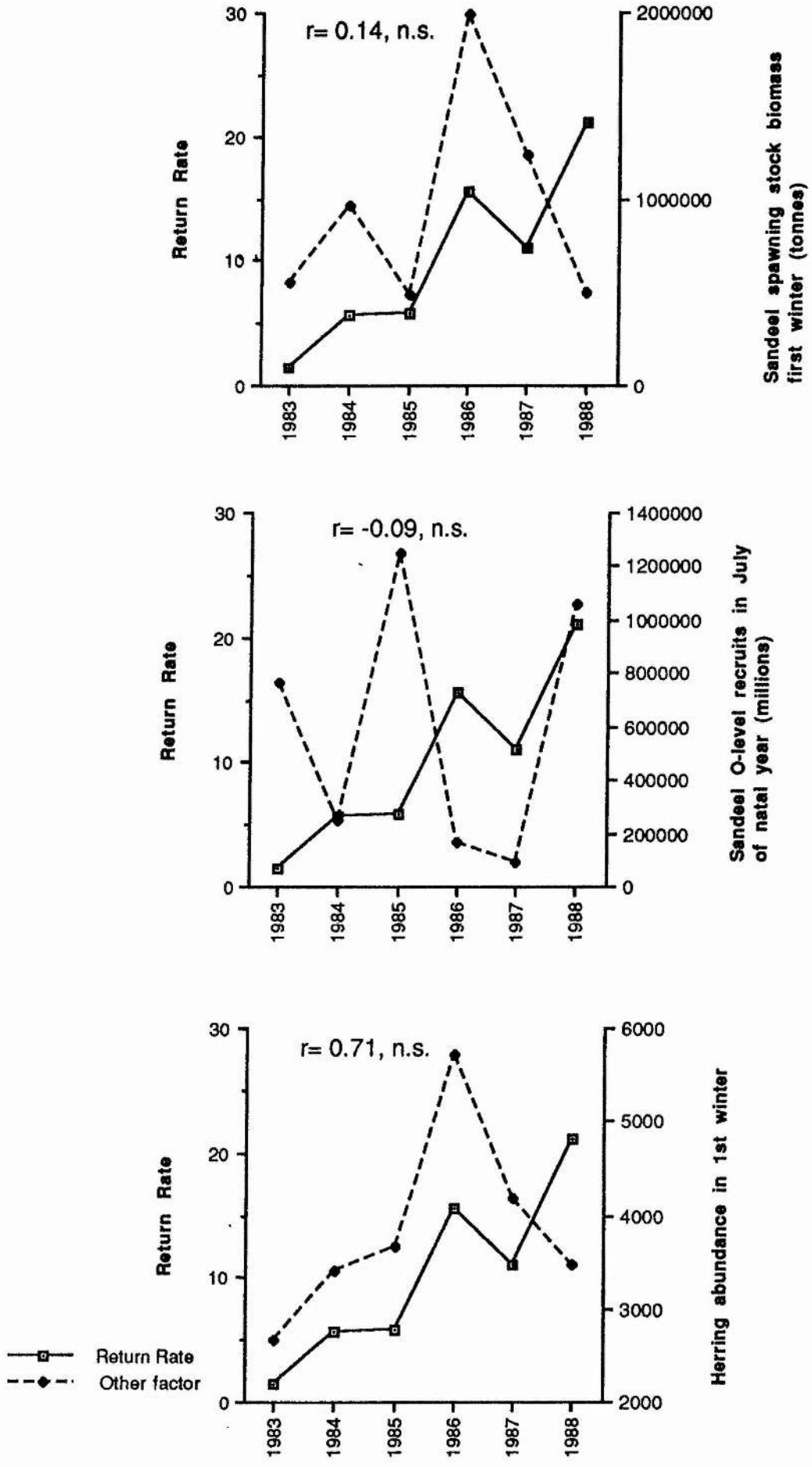

r= 0.14, n.s.
Return Rate
Daily intake (kJ)
r= -0.14, n.s.
Return Rate
Daily intake (g)
r= 0.03, n.s.
Return Rate
Value of fish per feed (kJ)
1983
1984
1985
1986
1987
1988
Return Rate
Other factor

Figure 3.6: Correlations between the percentage return rate of immatures by three years of age and measures of potential prey populations in July of the natal year (number of 0-level recruits) or during the first winter at sea (all other comparisons). Solid lines indicate return rate of birds hatched in that year, pecked lines the estimated prey population (see Methods). The r value and significance level of a Spearman Rank Correlation Coefficient (n=6 in all cases) is shown.


r= 0.14, n.s.
Return Rate
Sandeel spawning stock biomass first winter (tonnes)
r= -0.09, n.s.
Return Rate
Sandeel O-level recruits in July of natal year (millions)
r= 0.71, n.s.
Return Rate
Herring abundance in 1st winter
Return Rate
Other factor
1983
1984
1985
1986
1987
1988

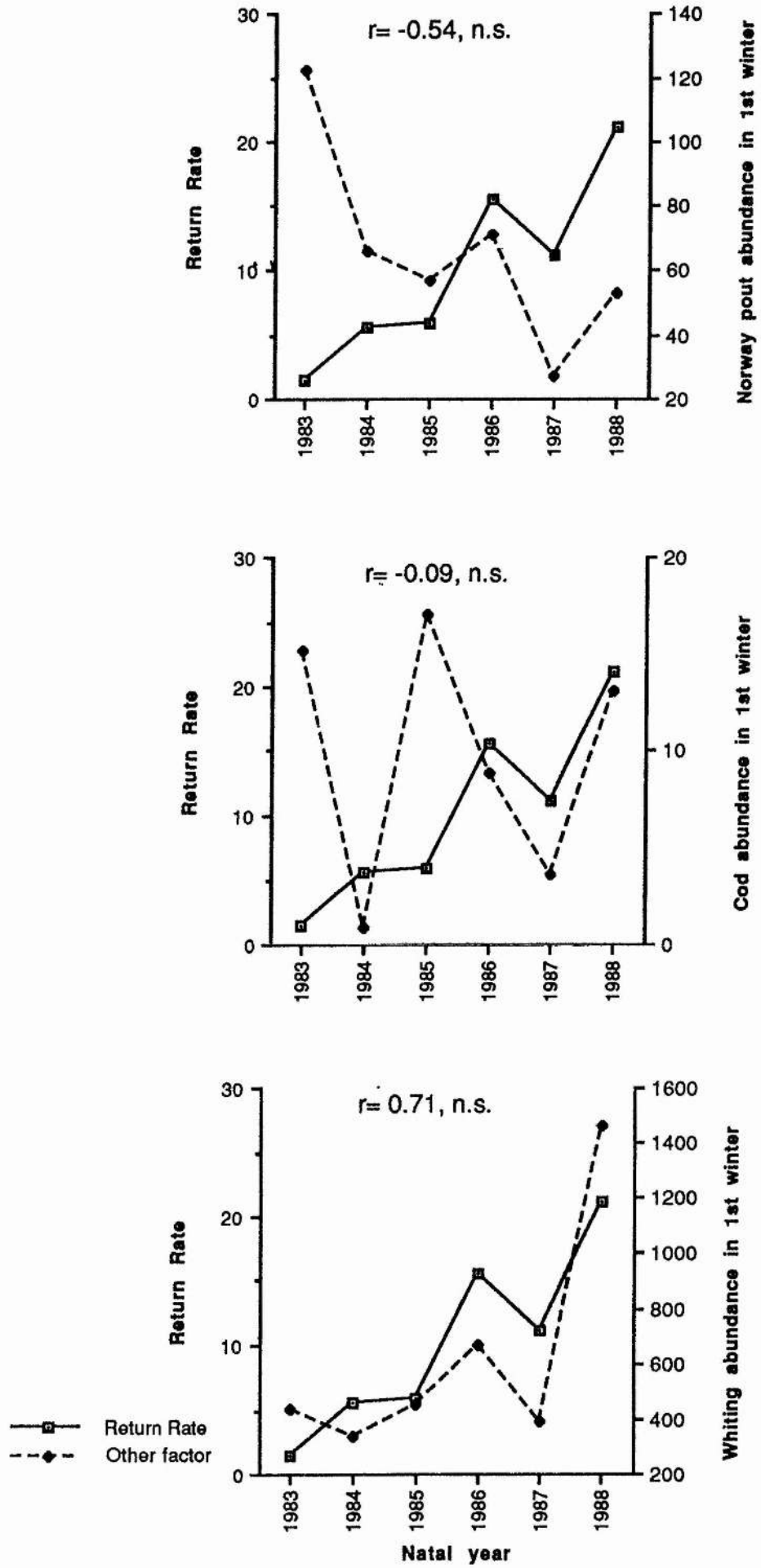
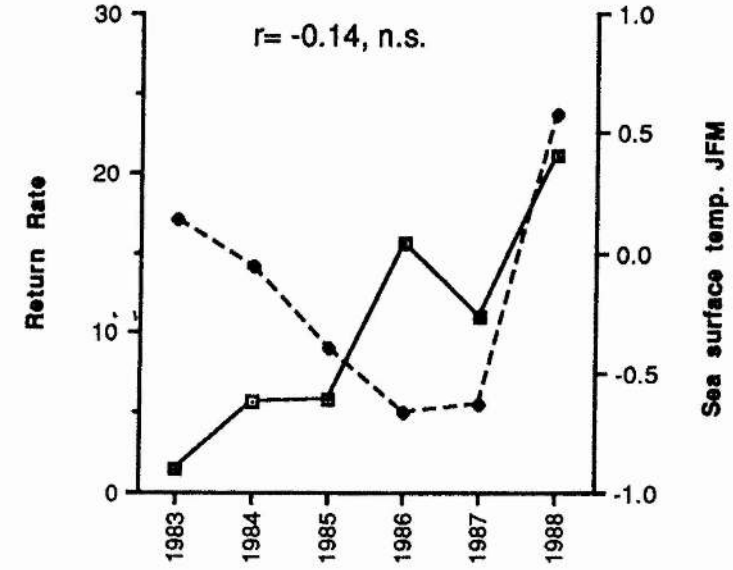
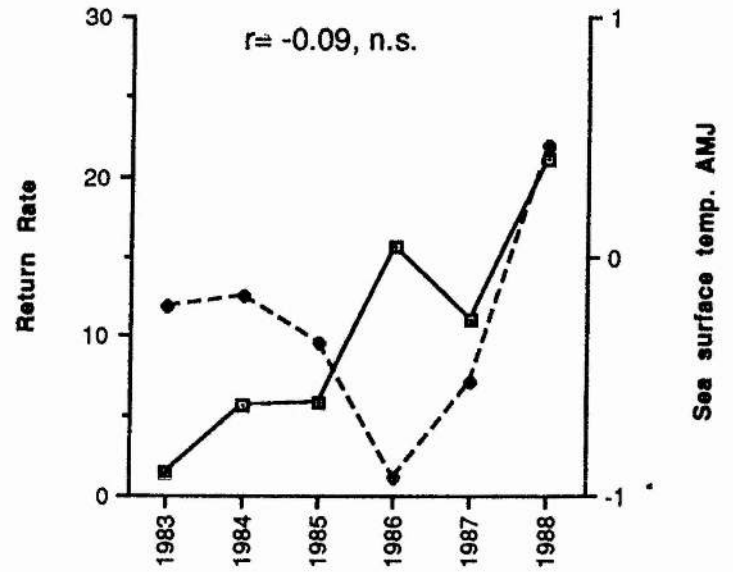
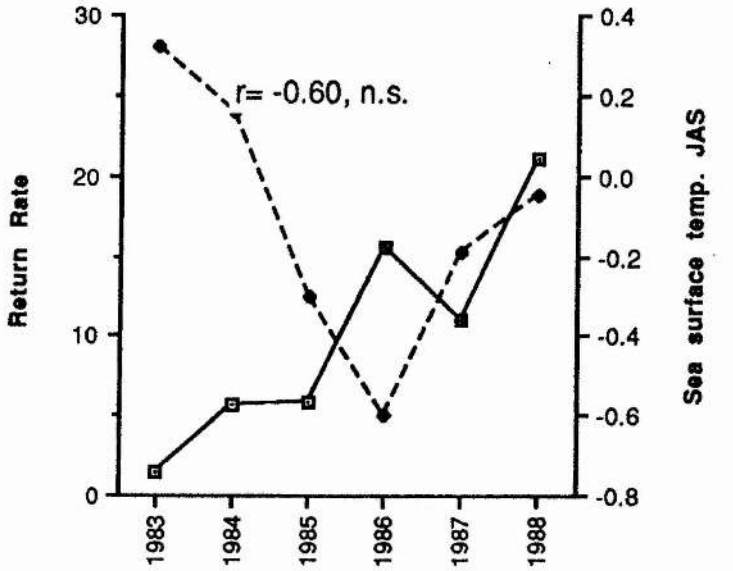

r= -0.54, n.s.
Return Rate
Norway pout abundance in 1st winter
r= -0.09, n.s.
Return Rate
Cod abundance in 1st winter
r= 0.71, n.s.
Return Rate
Whiting abundance in 1st winter
Return Rate
Other factor
Natal year

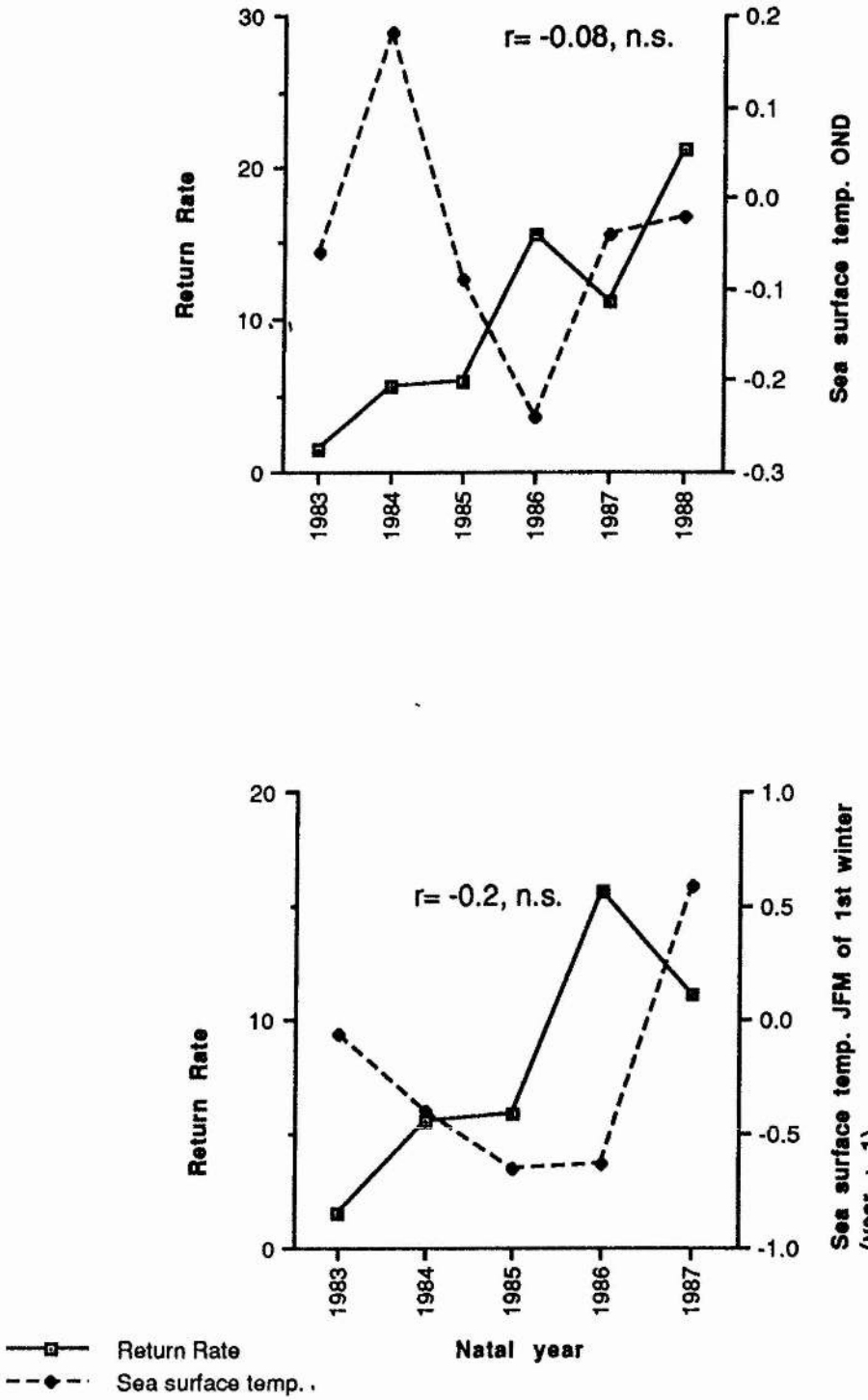
Figure 3.7: Correlations between the percentage return rate of immatures by three years of age and measures of sea surface temperature and gale force winds. Sea surface temperature is expressed as deviations from the seasonal average in Celsius, gales as hours of winds or number of days on which gale force winds occurred. Solid lines indicate return rate of birds hatched in that year, pecked lines sea surface temperature or gale force wind measures. JFM = January-March; AMJ = April-June; JAS = July-September; OND = October-December. The r value and significance level of a Spearman Rank Correlation Coefficient is shown (n=5 for sea surface temperature in JFM of the cohorts' first winter at sea; n=6 in all other cases).

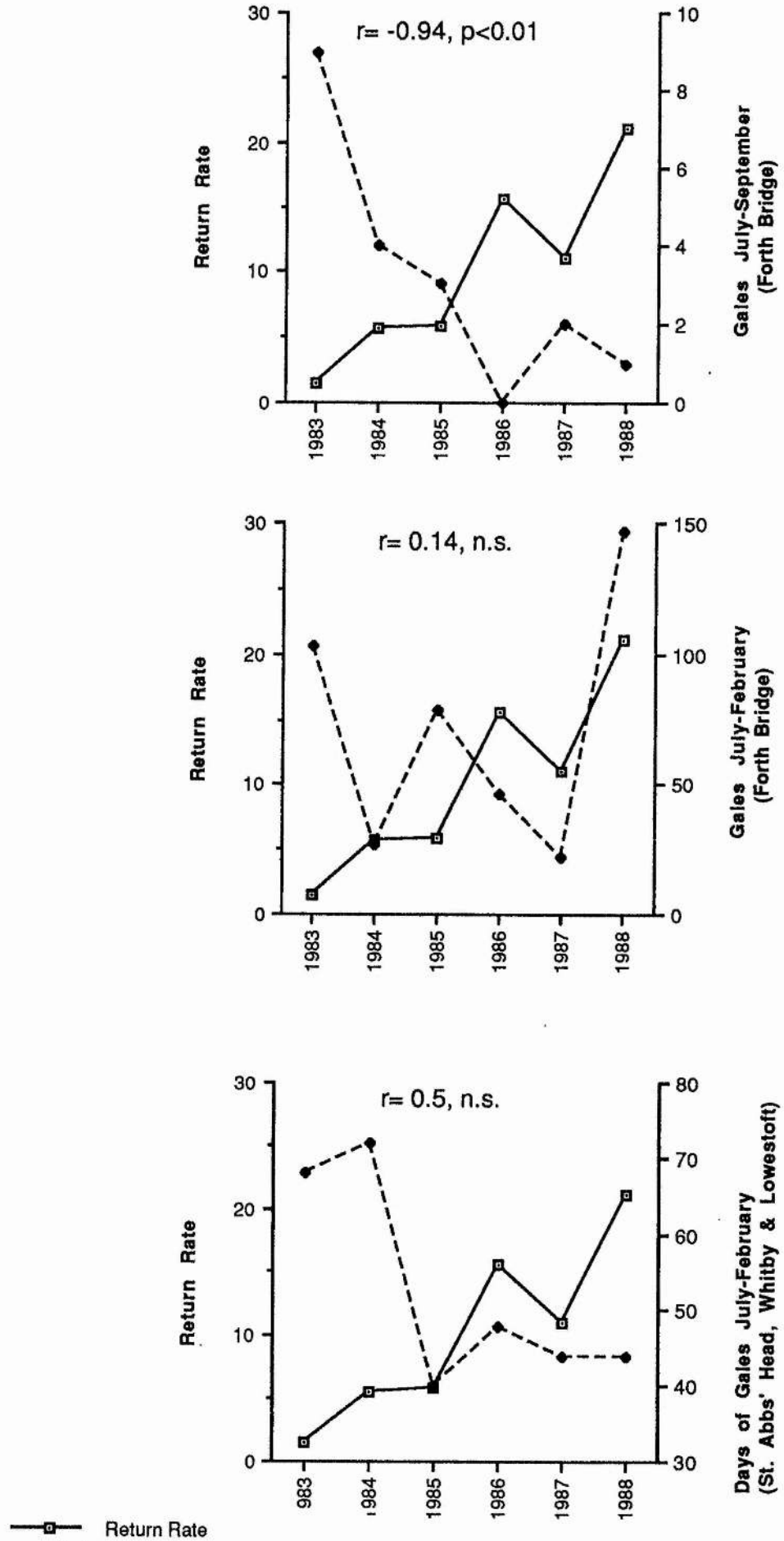






Return Rate
Sea surface temp.


r= -0.08, n.s.
Return Rate
Sea surface temp. OND
30
20
10
0
0.2
0.1
0.0
-0.1
-0.2
-0.3
1983
1984
1985
1986
1987
1988
r= -0.2, n.s.
Return Rate
Sea surface temp. JFM of 1st winter (year + 1)
20
10
0
1.0
0.5
0.0
-0.5
-1.0
1983
1984
1985
1986
1987
Natal year
Return Rate
Sea surface temp.


r= -0.94, p<0.01
Return Rate
Gales July-September (Forth Bridge)
r= 0.14, n.s.
Return Rate
Gales July-February (Forth Bridge)
r= 0.5, n.s.
Return Rate
Days of Gales July-February (St. Abbs' Head, Whitby & Lowestoft)
1983
1984
1985
1986
1987
1988
Return Rate
Gales

when the chick is at sea and dependent on its male parent (Spearman Rank Correlation Coefficient, r_s= -0.9, n=5, $p<0.05$). A prediction was made that this trend would continue for the 1988 cohort (3 years old in 1991). As only one hour of gales occurred in the fledgeling period in 1988, the prediction was that the cohort would rank second in return rate. The result was close to expectations, the cohort ranking first. The correlation with this result added was highly significant (Spearman Rank Correlation Coefficient, r_s= -0.943, n=6, $p<0.01$; Figure 3.7).

3.4: Discussion

The return rates reported here must be regarded as minimal estimates of survival rate. Ring loss, birds which were not observed, and emigration will all tend to depress the apparent return rate.

Very few metal rings were lost, but many birds lost colour rings, largely as a function of age. Within a cohort, birds attending the colony more often may be more likely to lose their rings as they will suffer more abrasion. Younger birds attend the colony less often than older birds (Chapter 4), so that if ring loss does affect visibility younger birds which have lost rings are presumably more likely to be missed altogether, reducing the apparent rate of ring loss. The sample sizes of older cohorts are small. Nevertheless, the effect is sufficiently strong to conclude that ring loss does increase steadily with age.

However, colour ring loss appeared to have little effect on detectability. Within a cohort birds varied widely in the number of sightings, which may have masked any effect, but the trend ran contrary to the predicted direction (ring loss reduces detectability) for some age classes. Overall there may be a slight reduction in observability with ring loss. If this is the case, the bias would be towards reducing the average number of times older cohorts were seen. Since birds were seen

progressively more often with age, this suggests that ring loss is not enhancing the probability of producing Type 1 errors. Observation probability was not affected by whether a bird bore a plain colour ring or one with an engraved identity number; field experience indicated that engraved rings speeded up identification rather than making identification more likely. Overall, ring loss appeared to be a minor factor in reducing apparent return rates.

It is extremely difficult to estimate the absolute survival of different cohorts, as both the proportion of surviving birds attending the Isle of May which were missed and the rate of emigration are unknown. Any attempt at adding a correction factor would be a guess. However, the measured return rates offer clear minima based on counts of known birds. The data on known survival in relation to the replacement rate needed to produce a stable breeding population are of limited value since the factors above would tend to lead to underestimates of survival rate. Where the measured return rate was less than the replacement rate it was usually by a small margin. It seems likely, therefore, that actual survival equalled or exceeded adult replacement levels in most years, and was greatly in excess in the 1986 and (unless mortality between the ages of 3-5 is unprecedentedly high) 1988 cohorts.

Previous attempts to measure survival rates in this species have depended on less direct measurement. Birkhead & Hudson (1977) used the maximum number of birds of known age seen in one day as an estimate. Since only a minority of Isle of May immatures were observed on any one day (Chapter 4), and birds were sometimes not seen until many years old, this measure probably underestimated survival rate greatly. Hatchwell & Birkhead (1991) estimated survival rate by calculating the rate necessary to produce observed population trends in the Skomer population. This assumed a demographically closed colony with negligible immigration and emigration, which in the light of data from this study (Chapter 7) may be suspect. The production of reasonably accurate absolute measures of

survival rates will depend upon accurate measurements of both return and emigration rates.

The ranking of return rates seems to be robust to biases caused by missed birds, since the proportion of birds ever seen rose progressively with cohorts hatched in later years, although there were fewer opportunities to observe them. Whether emigration rates varied between cohorts is unknown. Assuming they did not vary widely, it is reasonable to conclude from the data that survival rates also varied considerably, and that the ranking of return rates reflected relative survival rates between cohorts. Significant variations between immature cohorts in survival rate have also been found in wandering albatrosses (Croxall *et al* 1990).

The large variations in return rate suggest that models of guillemot population dynamics which assume a constant, or average, survival rate should be treated with caution. Rates of known mortality are low, depending entirely on ring recoveries. The rate of recovery is probably biased by the levels of human population on the shores where corpses are cast up, and the levels of fishing activity (guillemots are frequently drowned in nets) and hunting (still practised in the Faeroes and Iceland); and by the level of awareness of ringing. Birds dying far from the nearest shore, or which are taken by predators, are less likely to be recovered (Mead 1974). The results do indicate a very wide dispersal of immatures, from northern Iceland to northern Spain, with concentrations in the Skaggerak and Kattegat and off the Dutch coast, a pattern similar to that for the northern and eastern British population as a whole (Mead 1974).

The distribution, level and cause of death of immature guillemots recovered has varied with time both on Canna and the Isle of May (Swann *et al* 1989; Harris & Bailey 1992); but on the Isle of May the rate of recoveries is not predictive of the subsequent return rate, and indeed trends in the opposite direction to that which

would be predicted if ring recovery rates were a measure of overall cohort mortality. Changes in the rate of recoveries between immature cohorts have been cited as indirect evidence of changes in cohort mortality levels, resulting in changes in subsequent breeding numbers (Swann *et al* 1989; Harris & Bailey 1992). This evidence casts doubt on these hypotheses. Why ringing recovery and return rates should be positively correlated is unclear. Perhaps changes in recovery rate reflect changes in the number of birds surviving the fledgling period, so that in years with high fledgeling survival more birds are "available" to die and be recovered subsequently; however, there is no data available with which to confirm or refute this hypothesis.

Two statistical issues affect the interpretation of correlations of ecological data with survival rate. The first is general, the second specific to the current data set.

First, the threshold of statistical significance is conventionally set at the .05 level. This means that a real effect can be concluded if there is less than one chance in twenty that the observed differences between samples are caused by random variation, and are not indicative of different underlying populations in the statistical sense (a Type 1 Error—Siegel 1956). Where repeated tests against the same data—survival rate in this case—are made, the chances of obtaining Type 1 Errors are increased. Significant effects should therefore be assessed critically when found.

Second, return rate tended to increase with natal year. That is, over the study period, there was a tendency for those cohorts hatched in later years to show a higher return rate. For the cumulative return rate at 3 years old (the youngest age at which rank return rate between cohorts stabilised, and so providing the largest sample size) this effect was significant. This progressive change in apparent survival levels produces difficulties in later interpretation of correlates with survival rate. Clearly the year *per se* is not causally affecting survival probability, but *any*

progressively changing factor will be highly correlated with chick survival. Significant correlations which are found should, therefore, be examined carefully for supporting evidence before a causal relationship is suggested.

No measure of prey populations was found to be associated with survival rate. However, Harris & Bailey (1992) related changes in immature guillemot mortality in the 1980s to changes in sprat distribution and abundance. Unfortunately, sprat abundance was so low from 1984 that VPA analyses could no longer be carried out so that data for this species was unavailable for the period of this study. As sprat abundance remained low—though unquantified—throughout the period, while return rates climbed, a direct causal effect of sprat population size in winter on immature cohort survival rates seems unlikely. It cannot, however, be ruled out, especially as sprat distribution, which Harris & Bailey (1992) suggested might be an important factor, could have changed.

The correlation between cohort survival and the prevalence of gale force winds in the fledgeling period was highly significant. Full grown guillemots (and other auks) are vulnerable to storm conditions, which can produce spectacular "wrecks" of dead and dying birds on shorelines, particularly in autumn (Hudson 1985). It is not surprising that partly grown young, at sea and dependent on their male parent, may be similarly vulnerable as the strong correlation between gales and subsequent return (and presumably survival) rates suggests. This was the strongest correlation found between return rate and an environmental or ecological variable. Although the general trend was for gale prevalence to decline over the period 1982-88 (presumably coincidentally), the reversal of the trend in 1987 was parallelled by the lower subsequent return rate of the 1987 cohort. Additionally, the effect was predictive: the correlation was noticed in 1990, when it was also significant, and the ranking of the 1988 cohort (1st), available in 1991, was close to the predicted ranking (2nd). The results for 4 year olds were also significant. Despite the

difficulty of demonstrating causal effects between marine conditions and seabird survival, this suggests that adverse weather conditions in the fledgeling period (when the chick is at sea and dependent on its male parent) may be, for the Isle of May population at least, the primary factor affecting subsequent cohort size.

There is some theoretical and empirical evidence that mortality during this period can be particularly high. Ydenberg (1989) found that the fledging date of guillemots closely accorded with theory if going to sea were energetically necessary but considerably more dangerous than remaining at the colony. Gaston & Nettleship (1981) estimated that c. 40% of Brünnich's guillemot fledgelings died in their first three months at sea, a much higher rate than at any other period.

The direct agent of mortality due to adverse weather in this period is not clear. Adults do have difficulty in foraging in heavy sea conditions (Birkhead 1976), but both adults and dependent young at sea have considerable fat reserves (Harris *et al* 1992) and fledging weight is not related to subsequent survival (Hedgren 1981; Harris *et al* 1992), so that direct starvation is unlikely. Alternative hypotheses include exposure and/or separation of adult and chick leading to starvation.

Chicks from the Isle of May which went to sea early in both 1986 and 1988 were more likely to return to the colony as immatures than chicks fledging later in the season (Harris *et al, in press*). These were the two years in which there were the fewest gales throughout the period in which chicks were dependent at sea, and of the highest subsequent return rates. This may indicate that more developmentally advanced birds are at an advantage in density-dependent competition when cohort numbers are high in winter, the advantage disappearing when heavy mortality has occurred previously. Alternatively, since the effect found was not strong, perhaps only large sample sizes (from years when fledgeling period mortality was low due

to calm weather conditions, allowing a high subsequent return rate) attain statistical significance.

It is extremely difficult to show causal relationships between survival rates and ecological and environmental variables. However, given the lack of correlation between known death (ring recovery) rates and later return rates, the high correlation between return rate and weather conditions in the period when the chicks are at sea and dependent on their male parents, and the theoretical and empirical evidence for high levels of mortality among chicks during this period (Ydenberg 1979, Gaston & Nettleship 1981), an outline of life history factors and mortality in this period can be suggested.

Chicks go to sea at about three weeks old and 18-28% of adult body weight (Birkhead 1976; Hedgren & Linnman 1979), constrained to do so despite the increased mortality risk (Ydenberg 1979; Gaston & Nettleship 1981) because parents have increasing difficulty provisioning them adequately at the colony. At sea, close to food supplies, rapid growth is resumed (Harris *et al* 1992). Mortality in the three months that chicks are developing at sea varies widely depending on the weather conditions. Feeding is not normally a problem (Harris *et al* 1992), but chicks are vulnerable to exposure and/or separation from their parent during stormy weather. Mortality during this period is the primary factor influencing the ultimate size of a cohort. A number of other factors affect mortality later in the cohort's life history; from ringing recoveries it appears that most additional mortality occurs in the first year of life. Occasionally, catastrophic events such as oilings or "wrecks" may cause serious additional mortality (Birkhead & Hudson 1977).

If, as ssems likely, the main influence on cohort size is mortality at sea in the fledgeling period, this does not necessarily imply that the size of the breeding population is directly influenced. Greater numbers of surviving birds will

presumably come into greater competition at later stages of life. There may be increased competition for food in the winter, and Birkhead & Furness (1985) found that colonies of guillemots on promontaries and islands were larger than those on linear coastlines, which have smaller sea areas over which to forage. Larger colonies had lower rates of chick growth. These results suggest that density-dependent competition for food in the breeding season may influence the size of the breeding population. In such circumstances, a large cohort of young birds would face more intense competition for a limited number of breeding "slots" and the size of the breeding population would not be affected. Where few birds survive, however, there may be too few birds to fill the available "slots", resulting in a declining breeding population.

Harris (1991) suggested that the decline in the Isle of May breeding population in 1986-88 might be attributable to a low survival rate of immatures. Such evidence as is available is weak and equivocal. The known return rate (certainly an underestimate; see above) was below the theoretical replacement level for birds reaching 5 years old in 1988 (the 1983 cohort), However, breeding numbers increased between 1988 and 1989, when both the cohorts old enough to recruit had known return rates below replacement level. Changes in immigration rate and emigration rate not accounted for in the figures of known return rate (themselves probably related to levels of competition at the Isle of May and other colonies), and in prey availability, may also have influenced population levels. Quantification of all these variables will be necessary before accurate models of recruitment and population dynamics can be developed.

Further work should monitor the future correlations between return rates and factors which may be associated—sprat populations, and the prevalence of gale force winds in the fledgeling period. Quantification of the emigration rate, and

whether it can be treated as a constant between cohorts, is important if reasonably accurate absolute measures of survival rate are to be obtained.

Chapter 4

Attendance

4.1 Introduction

The long period of colony visiting prior to recruitment in most seabirds has provided a natural system in which the development of behaviour can be studied in detail (Danchin 1990 for a review). In the previous chapter, it was demonstrated that the proportion of an immature cohort which visited the colony increased with age; a number of studies have further shown that as seabirds age and/or gain experience, more time is spent at the colony both in terms of the length of season and/or the number of visits (e.g. razorbill (Lloyd & Perrins 1977); puffin (Harris 1983); pigeon guillemot(Nelson 1977); wandering albatross (Pickering 1988); kittiwake(Porter 1988) and Brünnich's guillemot (Noble 1990)).

The population of individually identifiable immature guillemots on the Isle of May provides an opportunity to investigate this area in some detail. This chapter describes the frequency and timing of visits to the colony by immature guillemots, and the influence of age and previous experience. The findings, and comparative data from other seabird species, are discussed in relation to the ecological and behavioural factors which may underlie the observed pattern of behaviour.

4.2 Methods

Immature guillemots were searched for from first light until the departure of the last birds from the colony (up to 4 hours later) during the 1989-90 winter. During the

summer field seasons in 1990 and 1991, data were collected in the course of the general fieldwork programme (Chapter 2).

Birds which recruited into the breeding population in the course of a field season were excluded from analyses of immature behaviour in that and subsequent seasons.

Arrival date was defined as the date on which an individual was first observed. Departure date was defined as the last date on which an individual was observed, where the bird had been observed more than three times in that season. Immatures were defined as experienced if they had been recorded (after their natal year) on the Isle of May in previous field seasons, or as inexperienced if they had not. Numbers of experienced birds in the 1986 cohort were large enough in 1991 to further subdivide experienced immatures into birds which had been seen in the 1990 breeding season and birds which had been seen in both the 1989 and 1990 breeding seasons.

The amount of time birds visiting the colony on a given day spent there (termed 'visit length' for convenience, although birds could have made trips to sea between observations) was estimated from the number of times birds were recorded during three-hourly repeated searches of the focal area of the colony in 1991. In the later part of the season, light conditions permitted an additional search commencing at 0300, although very few immatures (maximum 3) were present at that time. However, so that the number of opportunities a bird had to be recorded did not vary, records from this census have been excluded from analysis.

4.3 Results

4.3.1 Winter attendance

Immatures were not recorded in the 1989-90 winter (October—February), or in October 1984-87 (Harris & Wanless 1989), although adults were commonly present on breeding ledges in the mornings. In 1989, two birds bearing single blue rings were seen but were found to be adults which had lost rings from their full combinations. However, numbers of unringed birds of unknown age and origin did occupy top ledges used by immatures during the breeding season.

4.3.2 Seasonal attendance distribution

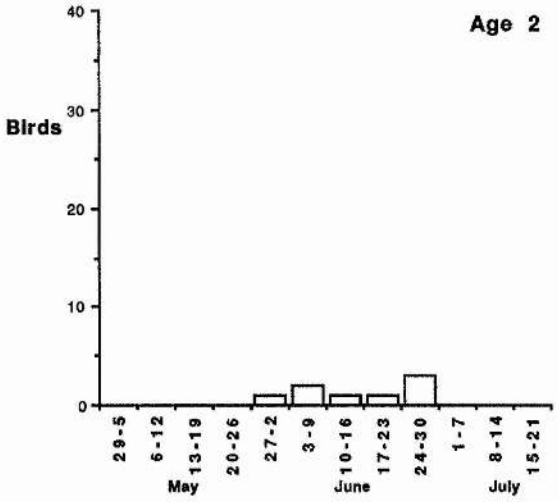
No immatures hatched in the previous year were recorded in either season.

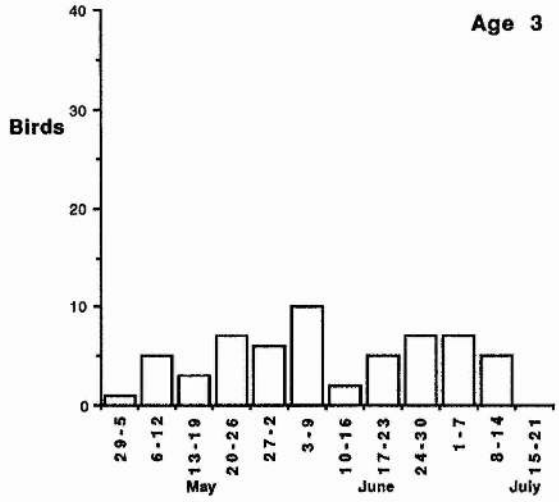
Figures 4.1a-k summarise the numbers of known individuals seen each week throughout the field season in 1990 and 1991. Overall, although the distributions for some cohorts were fairly flat, numbers tended to be highest in the nestling and early fledging period (mid June to early July), particularly in 1991. The rapid decline at the end of the season coincided with the general departure of postbreeders at the end of the season (no immatures were seen after 21st July in either year).

4.3.3 Arrival dates

Early individuals of the 1984 and 1985 cohorts were recorded in late March of 1990 and 1991; however, systematic observations did not begin until the beginning of the main field season in late (1990) and early (1991) April.

Figure 4.1 a-e: Age class and attendance levels - numbers of known individuals seen each week in 1990.


Age 2
Birds
40
30
20
10
0
29-5
6-12
13-19
20-26
27-2
3-9
10-16
17-23
24-30
1-7
8-14
15-21
May
June
July


Age 3
Birds
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30
20
10
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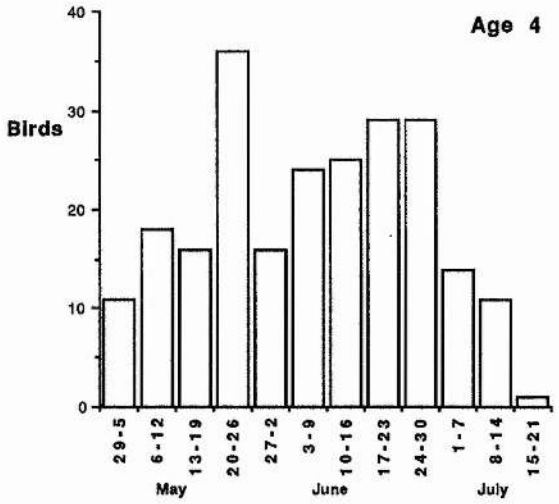
29-5
6-12
13-19
20-26
27-2
3-9
10-16
17-23
24-30
1-7
8-14
15-21
May
June
July


Age 4
Birds
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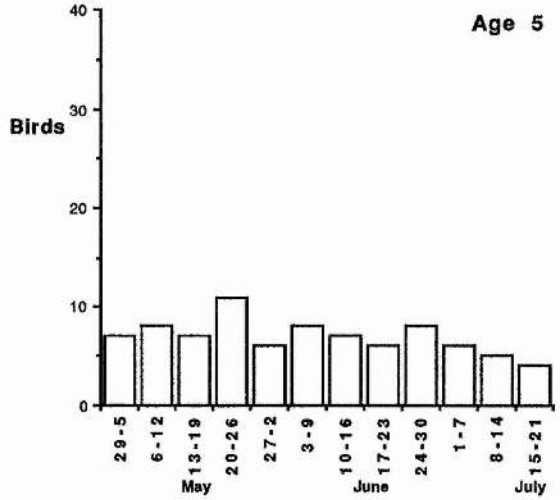
30
20
10
0
29-5
6-12
13-19
20-26
27-2
3-9
10-16
17-23
24-30
1-7
8-14
15-21
May
June
July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Birds
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29-5
6-12
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27-2
3-9
10-16
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24-30
1-7
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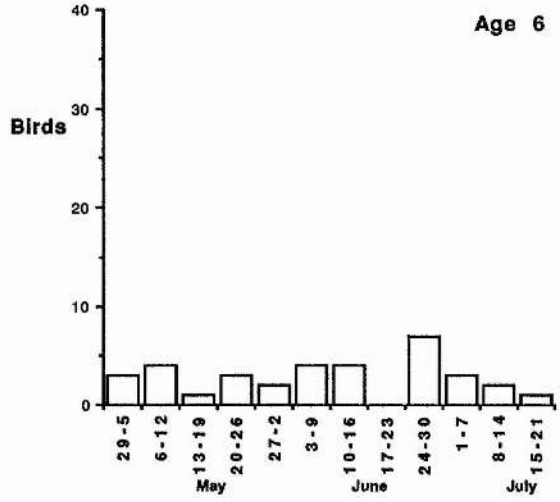
15-21
May
June
July


Age 6
Birds
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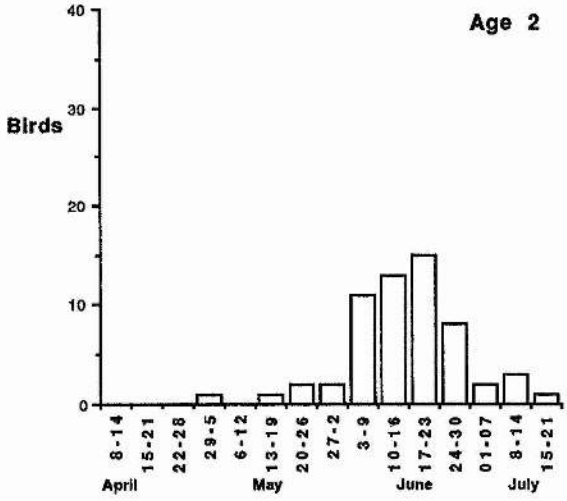
30
20
10
0
29-5
6-12
13-19
20-26
27-2
3-9
10-16
17-23
24-30
1-7
8-14
15-21
May
June
July

Figure 4.1 f-k: Age class and attendance levels - numbers of known individuals seen each week in 1991.


Age 2
Birds
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10
0
8-14
15-21
22-28
29-5
6-12
13-19
20-26
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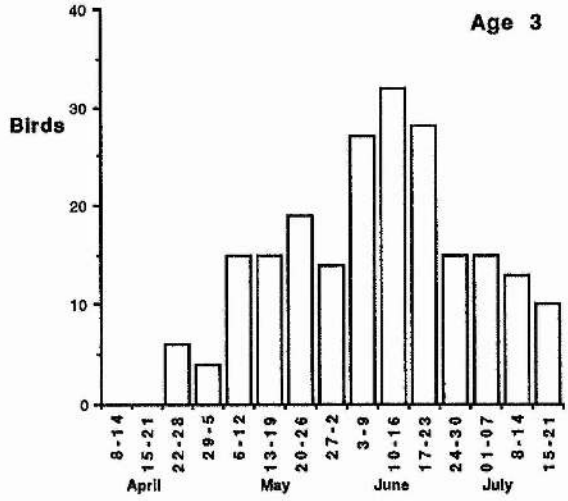
3-9
10-16
17-23
24-30
01-07
8-14
15-21
April
May
June
July


Age 3
Birds
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8-14
15-21
22-28
29-5
6-12
13-19
20-26
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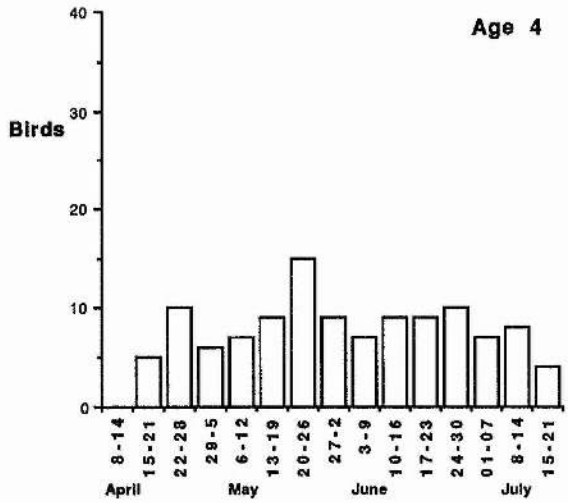
3-9
10-16
17-23
24-30
01-07
8-14
15-21
April
May
June
July


Age 4
Birds
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30
20
10
0
8-14
15-21
22-28
29-5
6-12
13-19
20-26
27-2
3-9
10-16
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24-30
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April
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June
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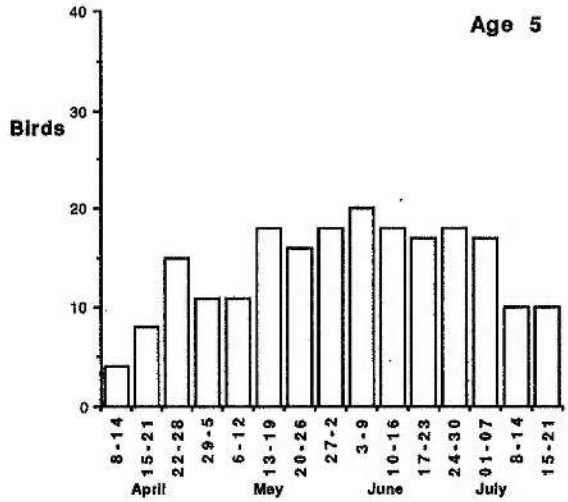
Age 5
Birds
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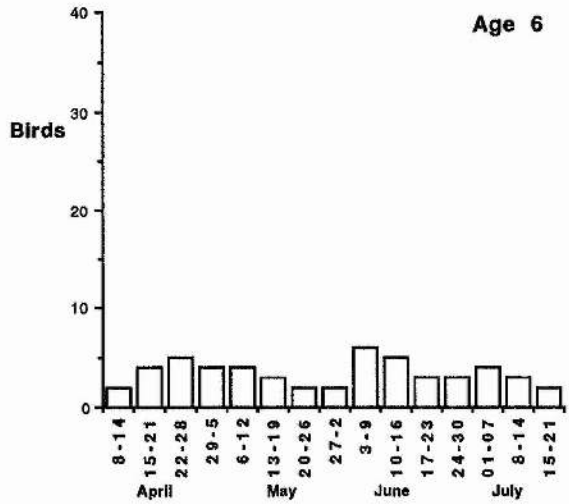
Age 6
Birds
40
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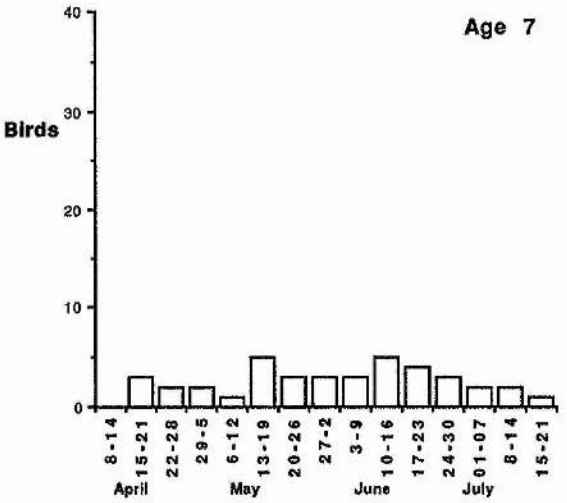
Age 7
Birds
40
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20
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0
8-14
15-21
22-28
29-5
6-12
13-19
20-26
27-2
3-9
10-16
17-23
24-30
01-07
8-14
15-21
April
May
June
July

The mean date of arrival became progressively earlier with age up to the age of 5 in 1990 and 4 in 1991. Two year olds arrived around the middle of June, corresponding to the early nesting period for most breeding guillemots; 3 year olds in early June, during late incubation; 4 year olds in late May in 1990 but early-mid May in 1991, during the incubation and laying periods respectively; 5 year olds in mid May, during incubation. Six year olds arrived later than 5 year olds, in early June, in 1990, but both 6 and 7 year olds arrived about the same time as 5 year olds, mid May, in 1991 (Figures 4.2a & 4.2b). There was an overall significant effect of age on arrival date in both years. Pairwise comparisons indicated that in 1990 the 3 year old cohort arrived significantly later than the 5 year old cohort, and the differences between 5 and 2 year olds and 4 and 2 year olds approached significance. In 1991 the 2 year old cohort arrived significantly later than all other cohorts, and the 3 year old cohort later than 4 year olds (Figure 4.2b).

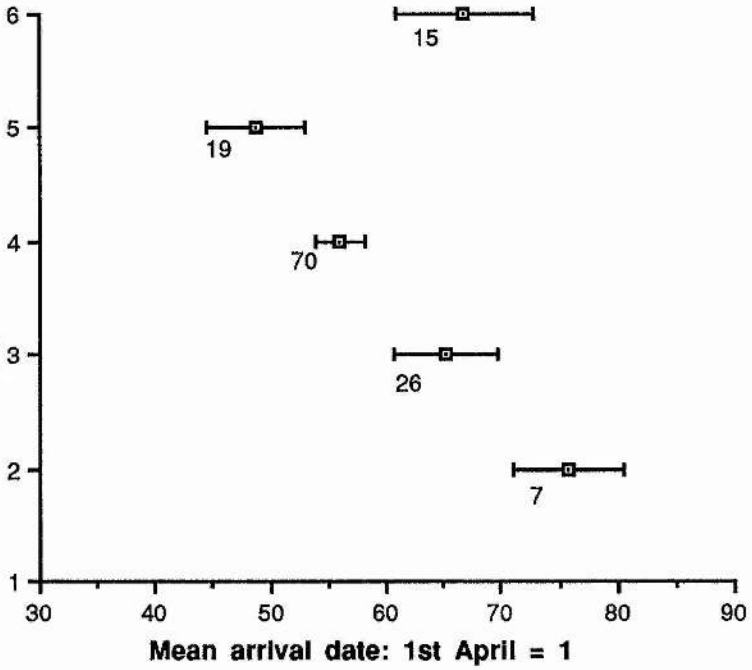
4.3.4 Departure dates

Departure dates varied little with age, centering around very late June and early July (the fledging period for most breeding birds). There were no significant differences between cohorts in either 1990 or 1991 (Figures 4.3a & 4.3b). None of the birds of the 2 year old cohort in 1990 were seen more than 3 times, so no figure could be given for the cohort. Some immatures remained up until the departure of adults, around the 20th July in both years (Figure 4.1).

4.3.5 Number of days recorded and duration of attendance

The number of days on which a bird was recorded (Figures 4.4a and 4.4b) and the duration of attendance (interval between first and last date where number of records >3: Figures 4.5a and 4.5b) were highly significantly correlated in both years (1990

Figure 4.2a: Age Class and Arrival Date (± 1 SE) in 1990

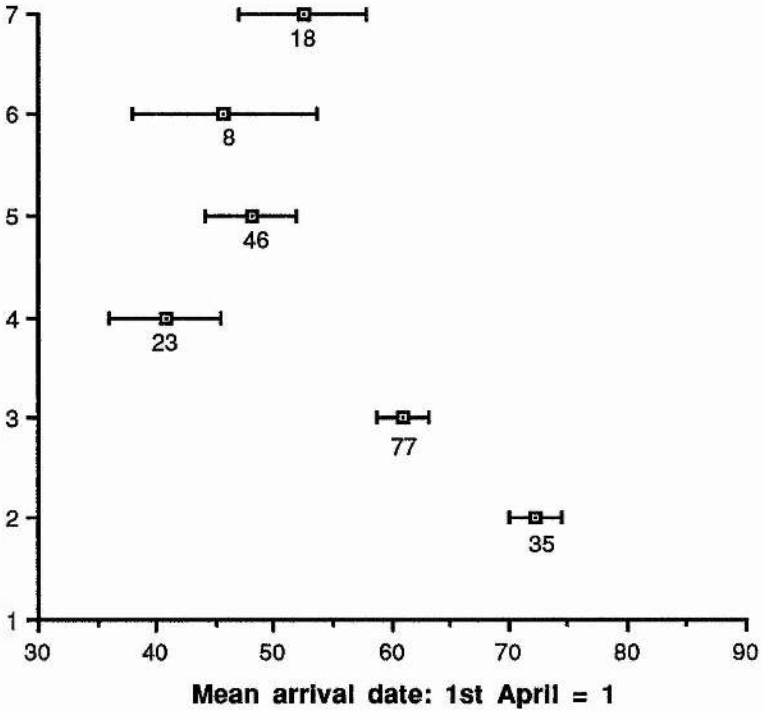


Kruskal-Wallis
H=16.3, 4d.f., p = 0.003

Multiple comparisons posthocs: 5 year old vs. 3 year old cohort significant, p<0.05. 5 year old vs. 2 year old and 4 year old vs. 2 year old cohorts approached significance (p<0.1).

n=number of birds

Figure 4.2b: Age Class and Arrival Date (± 1SE) in 1991



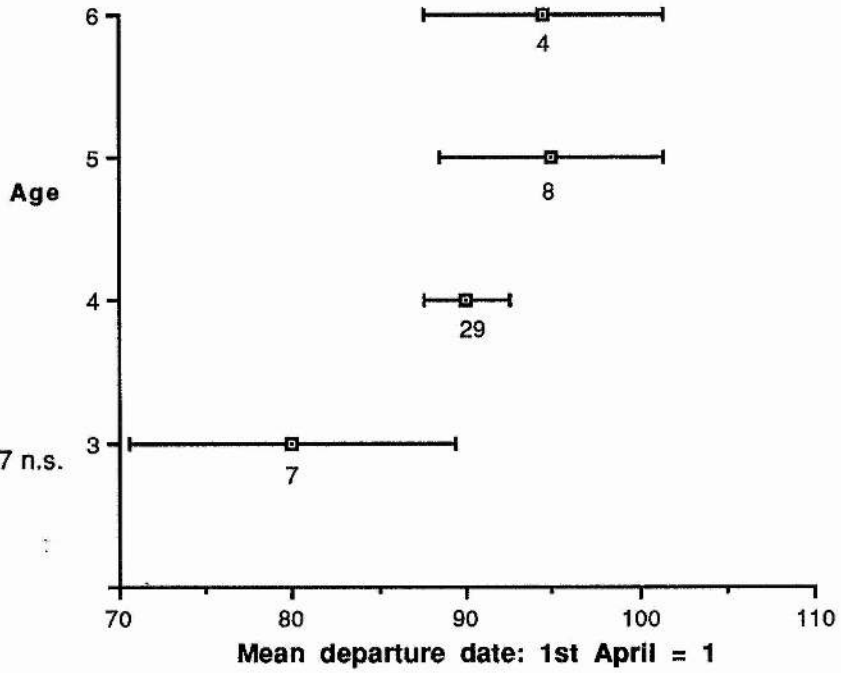
Kruskal-Wallis:

H = 30.9, 5d.f., p<0.0001

Multiple comparisons posthocs: 2 year old vs. 4, 5, 6 & 7 year old cohorts, 3 year old vs 4 year old cohorts, significant, p<0.05. All other pairwise comparisons n.s.

n=number of birds

Figure 4.3a : Age Class and departure date (± 1SE) in 1990

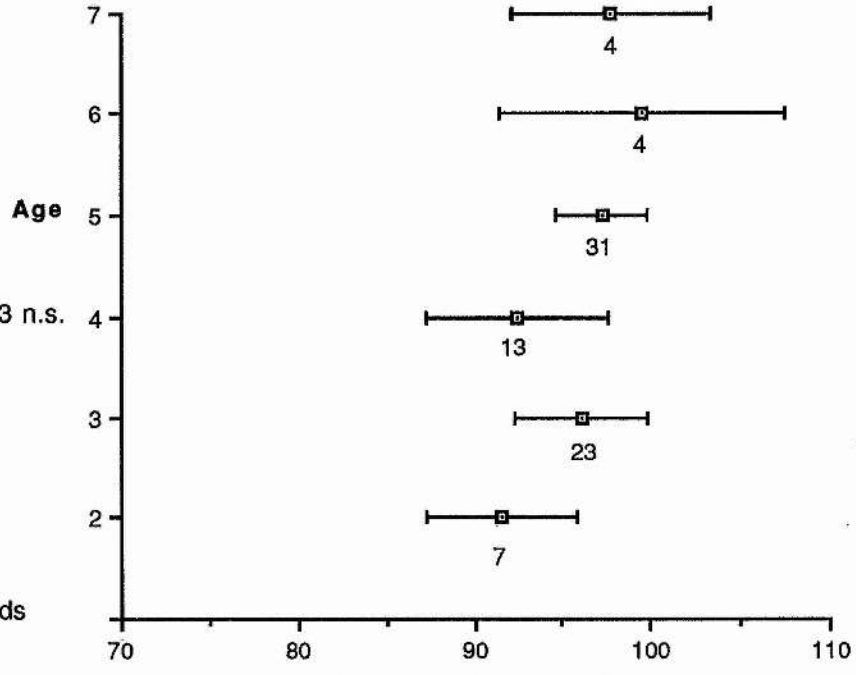


Kruskal-Wallis:

H=1.12, 3d.f., p = 0.77 n.s.

n=number of birds; all 2 year olds were seen <4 times.

Figure 4.3b: Age class and departure date (± 1SE) in 1991

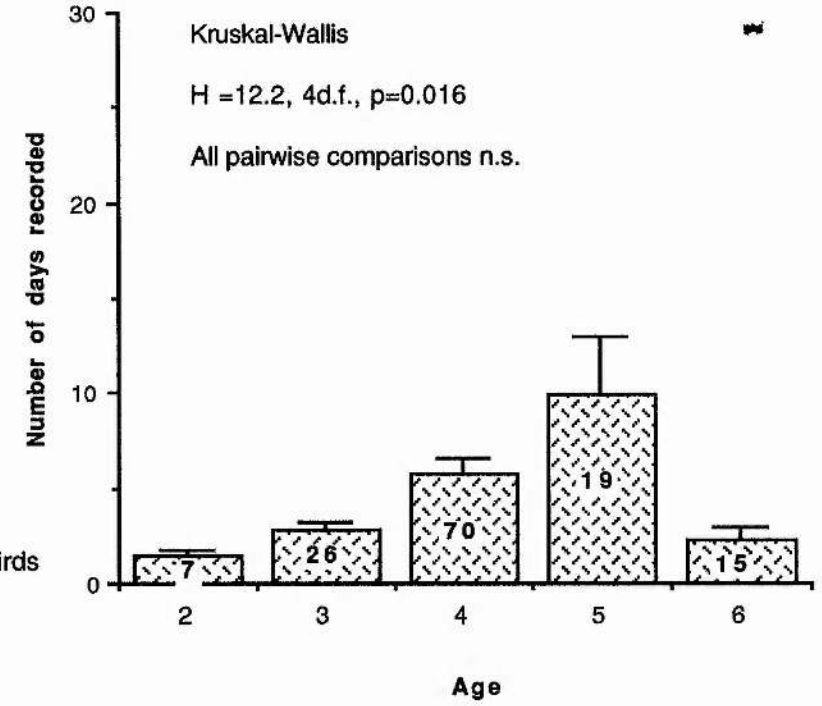


Kruskal-Wallis:

H=4.9, 5d.f., p=0.43 n.s.

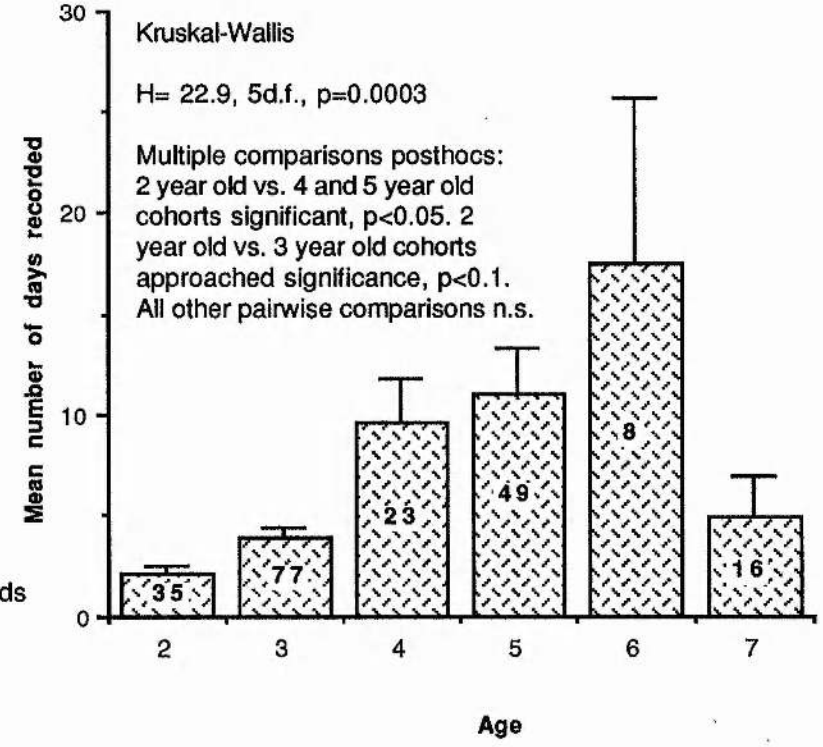
n=number of birds

Figure 4.4a: Age class and number of days recorded (± 1SE) in1990



n=number of birds

Figure 4.4b: Age class and number of days recorded (± 1SE) in 1991



n=number of birds

Figure 4.5a: Age Class and number of days between arrival and departure in 1990

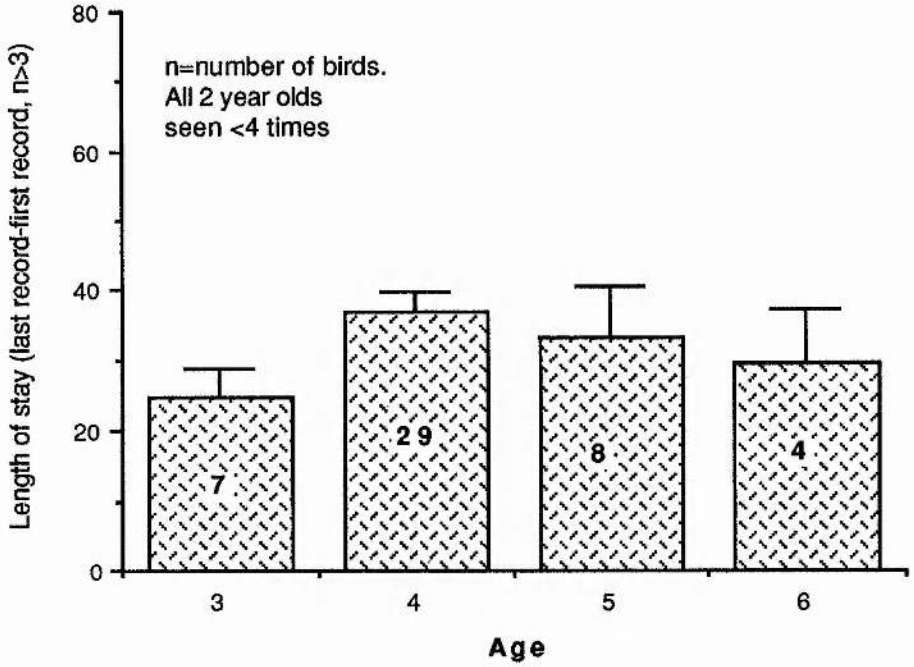


Figure 4.5b: Age class and number of days between arrival & departure in 1991

r=0.74, n=46, p<0.01; 1991 r=0.62, n=78, p<0.01). I have analysed the data further in the form of the number of observations.

There was a strong overall effect of age on number of records in both years (Figures 4.4a & 4.4b), with a trend in both years for the number of observations to increase progressively with age. However, the number of observations of birds of the 1983 cohort, 6 years old in 1990 and 7 in 1991, were at a level similar to 3 year olds in both years. No pairwise comparison was significant in 1990; in 1991 the youngest (1989) cohort present was recorded on significantly fewer days than both the 1986 and 1987 cohorts , and the comparison with the 1988 cohort approached significance.

4.3.6 Sex differences

Guillemot immatures are difficult to sex and sample sizes for each cohort were very small (Chapter 4). It was possible to test for sex differences in attendance parameters for 4 year olds in 1990; sample sizes for younger cohorts, and for 4 year olds in 1991, were too small, and most birds aged 5 and older which were of known sex were breeding. There were no significant differences between male and female 4 year olds in arrival date (Mann-Whitney, W=35, n_1(F)=5, n_2(M)=6, p=0.4 n.s.) or number of observations (Mann-Whitney, W=21, n_1=5, n_2=6, p=0.65 n.s.).

4.3.7 Experience effects

Birds were defined as experienced in colony attendance if they had been recorded in one or more previous seasons, inexperienced if they had not previously been recorded (see discussion). In 1990, no "experienced" 3 year olds were recorded; in 1991 sample sizes of the 6 and 7 year old cohorts were very small (partially due to

recruitment), and only one 6 year old and one 7 year old immature were inexperienced.

Arrival Dates

With the exception of 6 year olds in 1990, the trend in all ages in both years was for experienced birds to arrive earlier than inexperienced birds of the same age by between 10 and 30 days (Tables 4.1a & 4.1b). The overall effect was significant for all cohorts which were testable, except for 6 year olds in 1990 and 3 year olds in 1991.

Departure Date

As with age, experience appeared to have little effect on departure date. There was no consistent trend between cohorts for inexperienced birds to depart earlier or later than experienced birds, and differences in departure date were not significant for any age in either year (Tables 4.2a & 4.2b).

Number of records

The trend in all ages in both years was for experienced birds to be seen more often than inexperienced birds of the same age, the difference in the average number of sightings varying from 2 to 10 depending on the cohort (Tables 4.3a & 4.3b). The effect was significant for 4 year olds in 1990 and 5 year olds in 1991; the results for 3 and 4 year olds in 1991 approached significance.

Table 4.1a: Arrival date in relation to experience 1990

Age	Mean Arrival Date ±1SD				Mann-Whitney	
	Seen in previous season(s)	n	Not seen previously	n	W	p
4	15/5 ± 16.3	24	31/5 ± 7.5	54	598	0.0002
5	12/5 ± 19.1	8	23/5 ± 17.1	11	57	0.07[c]
6	6/6 ± 22.0	10	6/6 ± 28.2	5	77	0.76[c]

Table 4.1b: Arrival date in relation to experience 1991

Age	Mean No. Records ± 1SD						Significance	
	Recorded 1989 & 90	n	Recorded 1990	n	Not seen previously	n	Value	p
3	-	-	19/5 ±20.2	5	1/6±19.2	72	W=3026	0.19[ac]
4	-	-	4/5 ±19.8	14	25/5 ±23.0	9	W= 125	0.025[a]
5	3/5 ±20.2	9	15/5 ±30.2	18	11/6 ±23.6	15	H=11 2df	0.003[b]

[a] Mann-Whitney test

[b] Kruskal-Wallis one-way analysis of variance. Post hoc testing (Multiple comparisons test) indicated significant pairwise interactions ($p<0.05$) between birds not seen previously and both other categories

[c] n.s.

Table 4.2a: Departure date of immature guillemots in relation to experience in 1990

Age	Mean Departure Date ±1SD				Mann-Whitney	
	Seen in previous season(s)	n	Not seen previously	n	W	p
4	2/7 ± 13.7	15	25/6 ± 13.1	14	16	0.18 n.s
5	30/6 ± 21.7	5	10/7 ± 12.1	3	178	0.56 n.s

Table 4.2b: Departure date of immature guillemots in relation to previous experience in 1991

Age	Mean Departure Date ±1SD				Mann-Whitney	
	Seen in previous season(s)	n	Not seen previously	n	W	p
3	9/7 ± 9.9	4	4/7 ± 20.2	21	275	0.89 n.s
4	1/7 ± 16.4	10	11/7 ± 12.1	3	29	0.21 n.s
5	6/7 ± 14.6	29	7/7 ± 12.0	2	469	0.69 n.s

Table 4.3a: Number of records of immature guillemots in relation to experience in 1990

Age	Mean No. Records ± 1SD				Mann-Whitney	
	Recorded in previous season(s)	n	Not seen previously	n	W	p
4	10.5 ±10.6	22	3.6 ± 3.9	47	1048	0.0003
5	15.7 ± 5.7	9	4.9 ± 7.1	9	100	0.22 n.s
6	2.9 ± 3.0	10	1.2 ± 0.4	5	87	0.35 n.s

Table 4.3b: Number of records of immature guillemots in relation to experience in 1991

Age	Mean No. Records ± 1SD						Significance	
	Recorded 1989 & 90	n	Recorded 1990	n	Not seen previously	n	Value	p
3	-	-	8.3 ± 5.3	4	3.7 ± 4.2	73	W= 228	0.09[a]
4	-	-	12.6 ±11.1	14	5.2 ± 5.7	9	W= 80.5	0.08[a]
5	20.7±19.4	12	12.3 ±15.4	21	1.8 ± 1.6	14	H=14	0.001[b]

[a] Mann-Whitney test

[b] Kruskal-Wallis one-way analysis of variance. Pairwise comparisons (Multiple comparisons test) indicated a significant effect ($p<0.05$) between birds seen in 1989 and 1990 and inexperienced birds. The difference between birds seen in prevously in 1990 only and inexperienced birds approached significance ($p<0.01$).

4.3.8 Visit length

Assuming that cohorts did not differ in detectability, or propensity to move to sites outside the focal area of the colony (see discussion), the amount of time individuals spent there on days when they attended the colony (termed 'visit length') can be inferred from the number of times they were recorded in a day during weekly all-day repeated censuses of the focal area of the colony in 1991 (see Chapter 2).

The overall trend was for 5 year old birds to spend more time attending the colony (on days when they visited) than 3 or 4 year old birds in the early part of the season, but for there to be little difference between cohorts later in the season (Figure 4.6).

The difference between cohorts in visit length on 29 April (between 4 and 5 year olds only as no 3 year olds were seen) approached significance (Mann-Whitney, W=42, n_1=6, n_2=4, p=.07). Significant effects were found between cohorts on 9 May (Kruskal-Wallis, H=5.98, 2 d.f., p=0.05), 16 May (Kruskal-Wallis, H=7.7, 2 d.f., p=0.02) and 20 June (Kruskal-Wallis H=7.34, 2 d.f., p=0.03). There were specific pairwise differences between 4 and 5 year olds on 16 May (Multiple comparisons tests, $p<0.05$); all other pairwise comparisons were not significant.

The apparent decline in the length of visits to the colony among 5 year olds might have been due to a genuine decline in the visit length of individual birds, or to birds arriving later in the year having shorter average visit lengths thus lowering the cohort mean. Where birds were seen on at least one occasion both in the early part of the season (6th June and earlier) and the later part of the season (14th June and later), the mean visit length was taken for each period and compared in a Wilcoxon matched pairs test. The result indicated that visit lengths of individuals were shorter

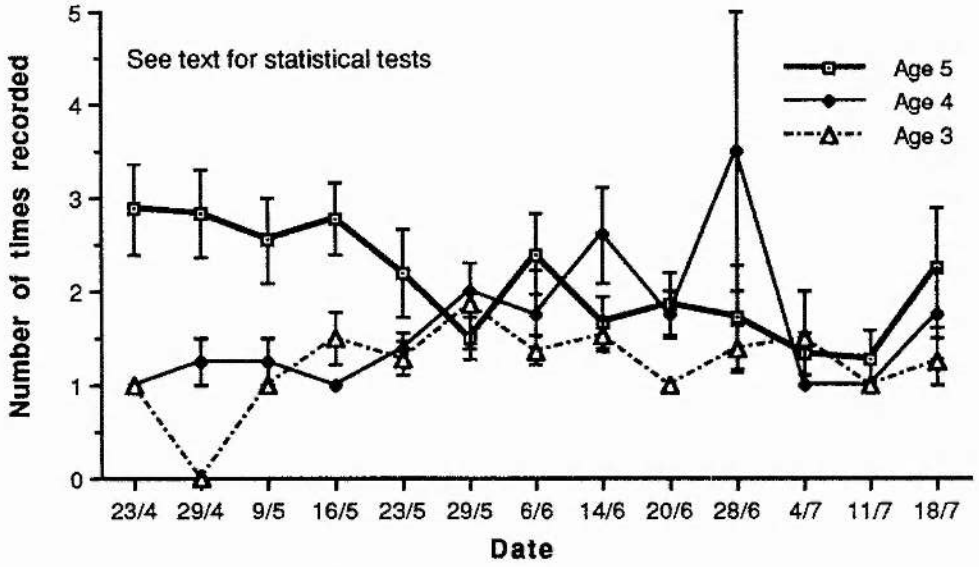


Figure 4.6: Age class in relation to the mean number of times birds visiting the Isle of May were recorded that day (± 1SE) during systematic all-day searches of the focal area of the colony.

Date	n Age 3	Age 4	Age 5
23/4	1	8	2
29/4	0	4	6
9/5	3	4	11
16/5	4	3	9
23/5	7	8	10
29/5	7	3	12
6/6	11	4	10
14/6	19	5	12
20/6	8	4	7
28/6	5	2	7
4/7	2	5	6
11/7	3	4	7
18/7	4	4	4

later in the season (Wilcoxon test, n=13, test n=10, T=7, p=0.04). Seasonal differences among 3 and 4 year old birds were not significant (3 year olds: Wilcoxon test, n=9, test n=6, T=10, p=1.0 n.s. 4 year olds: Wilcoxon test, n=10, test n=7, T=6.5, p=0.17 n.s.).

4.4 Discussion

The function of winter attendance in adult guillemots appears to be related to site maintenance and/or pair bond maintenance (Harris & Wanless 1989, 1990). These functions do not apply to immatures, which are siteless and unpaired, so there appears to be little positive reason for immatures to attend the colony overwinter. If they are relatively deficient in foraging ability, as is common in seabirds (Chapter 1), then they may also lack the energy reserves to permit attendance. Ringing recoveries (Chapter 3) indicate that immatures winter at long distances from the Isle of May.

The age and origin of the unringed birds present on top ledges overwinter is unknown. If they were immatures from the Isle of May, some at least should have been ringed. Possibly they are adults from elsewhere in the colony, or birds from other colonies which are wintering in the vicinity of the Isle of May. Taylor & Reid (1981) suggested that birds from other colonies might visit the Isle of May overwinter, but Harris & Wanless (1989) considered this unlikely, as marked adults were almost always found at their summer breeding sites in winter.

In broad terms, the pattern of attendance of immature guillemot cohorts can be described as follows: two year olds arrived around the early nestling period and were seen only a few times. Older cohorts tended to arrive progressively earlier in the season, and were seen more often, up until c. 5 years old, after which arrival and attendance levels stabilised (but see below).

There is a possible alternative explanation of the data. Older birds tend to be more sedentary than younger birds and to be found on sites in the colony rather than club sites on tidal rocks (Chapter 5). As a result, younger birds might have been more difficult to find and to identify than older birds. The effect of this would be to reduce the number of times younger birds were seen, even if they were attending the colony as frequently as older birds. This in turn would tend to produce a later (apparent) arrival date than in older cohorts. It seems unlikely, however, that such biases would produce an effect as strong as that observed. In addition, if such a bias were occurring, apparent departure dates should also have varied.

No differences were found in departure dates between cohorts, in line with studies of immature Brünnich's guillemots (Noble 1990). Departure coincided with the fledging period, as in Brünnich's guillemot (*op. cit.*) and razorbill (Lloyd & Perrins 1977), but some individuals remained until the mass departure of postbreeders at the end of the season, as in the puffin (Harris 1983).

This pattern of immature colony attendance is common among seabirds. Similar findings have been reported in wandering albatross (Pickering 1988), Adelie penguin (Ainley *et al* 1983), Manx shearwater *Puffinus puffinus* (Perrins *et al* 1973), gannet (Nelson 1978), kittiwake (Porter 1988), razorbill (Lloyd and Perrins 1973), Pigeon guillemot (Nelson 1987) and Brünnich's guillemot (Noble 1990, Gaston 1991). Birkhead and Hudson (1977) and Hudson (1979) also concluded that guillemot immatures arrive at the colony at earlier dates as they age, based on the earliest sightings of birds of known age.

An exception to the pattern outlined above is the attendance behaviour of the 1984 cohort, 6 years old in 1990 and 7 in 1991. In 1990, the mean date of arrival for this cohort was during the later incubation period of the breeding cycle, similar to that of 3 year olds; in both years the number of observations were more similar to 3 year

olds than to those of older cohorts. The reasons for this pattern of behaviour are not clear. Loss of colour rings reducing detectability is not likely to have been a major source of error (Chapter 3). The survival rate of guillemots from this cohort appeared to be very low, probably because of environmental conditions early in the first year of life (Chapter 3). Dietary quality early in life is very strongly correlated with later fitness and reproductive success in primates (Altmann 1991) and to a lesser degree in red deer *Cervus elaphus* (Clutton-Brock *et al* 1987); it is possible that the general fitness of survivors of the 1984 cohort was similarly affected by the adverse conditions that killed most of their cohort. Alternatively, as most guillemots on the Isle of May appear to recruit at age 5 or 6 (Chapter 6), if most of the 1984 cohort had recruited, the remnant immatures of this cohort which were unable to breed during the study may have been relatively unfit individuals.

There has been little previous work on the effect of experience on immature attendance patterns in seabirds. Pickering (1988) found a direct effect of experience on attendance parameters in immature wandering albatrosses; as experience increased, albatrosses returned to the colony earlier each year and spent more days ashore. This appears to be the first demonstration of a similar effect in alcids, although Noble (1990) suggested (without statistical analysis) that arrival date was related to experience in Brünnich's guillemot.

An assumption of this data is that there was no systematic bias against observing particular individuals so severe that they were *never* observed, though present, in earlier years, and then recorded with lower efficiency in subsequent seasons. This might occur if such birds consistently occupied sites which were difficult to observe. However, as young birds were usually first recorded on club sites and moved to sites in the colony in later years and later in the season (Chapter 5), it is unlikely that this is an important effect.

Also, if there is a sex difference in the age of first return to the colony, as appears possible (Chapter 4), apparent experience effects could be due to differences between sexes in behaviour. This seems unlikely because the sex difference, if it occurs (the effect was not significant and might have been due to younger males being more easily sexed), appears to be weak in comparison to the strength of some of the experience effects. Also, there were no sex differences in arrival date or number of observations among 4 year olds in 1990, where the sample size was sufficient for testing.

Assuming, then, that these results do indicate an effect of experience on colony attendance parameters within cohorts, much of the variation between cohorts may reflect experience (which will be closely correlated with age) rather than age *per se*. Alternatively, both greater levels of experience (attendance at an earlier age), and enhanced attendance (and recruitment: Chapter 6) levels, may be secondary reflections of the underlying quality of individual birds. Variations in individual quality appear to affect many aspects of the recruitment process in kittiwakes (Wooller & Coulson 1977; Porter 1988, 1990).

The data on attendance levels within a day indicates that the average visit length of 5 year old birds was longer than that of younger birds in the early part of the season, but subsequently declined. Younger birds did not vary significantly in visit length between the early and late parts of the season. The period of longer visiting coincided with the prelaying and laying period in the colony as a whole. Breeding opportunities were potentially still available, and it seems likely that 5 year old birds were assessing or pursuing opportunities to recruit into the breeding population, or possibly if male to gain EPCs. Many birds of this cohort (excluded from the analysis) did recruit; no bird from a younger cohort did so (Chapter 6). Later, with no prospect of recruitment until the next season, attendance for such extended periods in a day would no longer be advantageous. There may also be costs

involved in extended visiting, as birds cannot feed while at the colony; in particular, long periods of attendance may not be sustainable without using up reserves, which become depleted as the season progresses.

Longer visits early in the season, relative to other cohorts, are likely to increase chances of detection and so both increase the number of records and produce an earlier mean arrival date than would be found otherwise. It is difficult to assess the strength of this effect as the chances of seeing a bird when it is present are not quantifiable; if detection rate is reasonably high, then the bias due to variations in visit length will be relatively small; if low, relatively large. In either case, the conclusion that older birds devote greater amounts of time overall to colony attendance is unaffected.

In summary, a general advancement with age in the date of arrival at the colony and in the number of days the colony was visited appears to occur up to the age of about 5 years, the age at which birds begin to recruit in substantial numbers. There is evidence of an effect of experience, separate from age, on attendance variables; much of the age variation may reflect increased average experience rather than a direct effect of age. Alternatively, fitter birds may both return to the colony at a younger age and show enhanced attendance levels in subsequent years. Five year old birds visited the colony for longer periods than 3 and 4 year olds in the early part of the season; this may have been connected with attempts at, or assessment of opportunities for, recruitment.

Chapter 5

Dispersion within the colony: club and subcolony attendance, and intracolonial philopatry

5.1 Introduction

Immature seabirds are not distributed randomly within a colony. For example, wandering albatross males spend more time in the vicinity of their nest site as they become older (Pickering 1988); puffin immatures are more likely to be found defending or investigating burrows as they age, and are often found close to the burrow from which they fledged (Harris 1983). In many species, immature birds form groups known as clubs on sites adjacent to, or on unoccupied areas within, breeding colonies (e.g. herring gull, Tinbergen 1953; great skua, Davis 1976; Klomp & Furness 1991; gannet, Nelson 1978); in others, immatures are typically dispersed among adult birds (e.g wandering albatross, Pickering 1988; Manx shearwater, Perrins, Harris & Britton 1973; puffin, Harris 1983). In some senses, guillemots are intermediate between these two extremes since large numbers of immatures congregate at club sites, but many others are found on, or above, the breeding colony itself (Birkhead & Hudson 1977).

The fact that immature seabirds, and in particular guillemots, are not distributed randomly within the colony, or randomly in the areas accessible to them where adults are territorial, implies that understanding the factors underlying the distribution of immatures within the colony may be of some importance. This chapter describes the distribution of immature guillemots within the colony and

discusses the implications of the pattern of distribution in relation to recruitment processes and to the function of colony attendance.

5.2 Methods

Definitions of subcolonies and clubs, and general fieldwork methods, are outlined in Chapter 2. The location of birds was noted each time they were observed. The populations of clubs were counted twice daily along the focal area of the colony between Lady's Bed and Green Face, commencing at 0600 and 1700 GMT. Weekly averages and standard errors were obtained by taking the mean of all counts. Bad weather occasionally prevented counting, but never for more than two censuses in a week.

Intracolonial philopatry is the propensity of immature birds to attend the colony, or for recruits to breed, at sites closer to their natal site than would be expected if birds were distributed within the population at random. The precise natal location of immatures ringed as chicks was not recorded; ringing location was classified by subcolony. Individuals were therefore defined as attached to a subcolony where the majority (>50%) of visits to the colony (i.e. excluding visits to clubs) were to that subcolony. Birds attached to their natal subcolony were considered philopatric. A few birds could not be classified as primarily attending one colony; these were termed unattached, and were by definition non-philopatric.

A major problem with assessing levels of intracolonial philopatry is that subcolonies may differ in "attractiveness" to immatures for reasons such as the availability of a wide top ledge above the breeders, or some other physical or social factor not readily detectable by researchers. This is a particular difficulty where both a large proportion of birds attend one subcolony and a large proportion were ringed

there, as in the case of Colony B in this study. To avoid a spurious conclusion of philopatry, some measure allowing for subcolony attractiveness must be devised.

One method of achieving this is to compare the actual frequencies of philopatric birds with the expected frequencies if birds were choosing subcolonies without respect to natality. In the present case, this can be achieved by calculating the proportion of all subcolony-attending immatures (or recruits) that were attached to a particular subcolony, and from that calculating the number of immatures (or recruits) hatched at the subcolony which would be found there if attachment were in proportion to the fraction of the population as a whole which attended that subcolony.

Mathematically, this relationship can be expressed as:

$$\text{Expected Frequency} = \frac{\text{No. birds attached to subcolony}}{\text{Total birds seen}} \times \text{No. birds natal to subcolony seen}$$

So, for example, in 1991, 134 eligible (see below) immatures of known age and origin were observed. Of these 32 were attached to Colony B. Forty-two colony-attending immatures hatched at Colony B were seen that year. Substituting these values into the equation, we obtain $E = (32/134) \times 42 = 10.03$, approximating to 10. This is the number of immatures hatched at Colony B which we would expect to be attached there if birds were selecting colonies without regard to natality; in fact, 26 of the 42 Colony B hatched birds were attached to the subcolony. In this way, an expected frequency for each subcolony at which chicks were ringed can be generated. The summed values for all subcolonies can then be compared with the actual values in a χ^2 test.

An assumption of this model is that adequate observations could be made at all subcolonies. This was clearly not the case with the Maidens subcolony, which was located on rocks facing out to sea on an islet accessible only at low tide. Birds with cohort colour rings were sometimes seen on the Maidens from the main island, but the ring numbers could not be read. Conversely, birds ringed as chicks on the Maidens were frequently at other subcolonies. Three recruits (all hatched on the Maidens) were found on the Maidens subcolony in the course of ringing operations. However, 8 were observed breeding elsewhere. This level of observed recruitment philopatry in Maidens birds was significantly lower than in the rest of the population (χ^2=2.586, 1 d.f., $p<0.05$), and was probably due to lower detection rates at the Maidens. Accordingly, all birds hatched at the Maidens subcolony have been excluded from immature and recruitment philopatry analyses.

Birds which recruited in a given field season, and birds seen only on clubs (where birds did not breed), were also excluded from analyses of immature philopatry. Immatures were defined as experienced if they had been recorded (after their natal year) on the Isle of May in previous field seasons, or as inexperienced if they had not.

5.3 Results

5.3.1 Attendance at clubs

Clubs in the focal area of the colony varied from large, regularly occupied areas such as the Pilgrim stack or the tidal rocks below Green Face, through smaller intertidal ledges such as those below Colony 4 and Dense, to small and irregularly occupied niches along the length of the focal area. All were on intertidal rocks or in the splash zone, and all were accessible directly from the sea. Birds usually swam

up to clubs, rarely flying to them. Consequently, the attendance at different clubs was related to the state of the tide.

Seasonal changes in the numbers of birds attending clubs in the focal part of the colony are shown in Figure 5.1. Records of numbers at clubs were not collected systematically in the early part of the 1990 season, so I have used data from 1991. Numbers reached a peak in late May and early June, corresponding to the later incubation and early nestling period of the breeding cycle. Data from the latter part of the 1990 season showed a similar pattern to the data from later 1991. A whole island count was made at mid-tide on 12th June 1991, just after the peak in attendance; 797 birds were counted.

Most birds natal to the Isle of May which visited clubs were 2-3 years old (Figures 5.2a & 5.2b), numbers declining to very low levels from the age of four. One adult, which had bred unsuccessfully that year, was seen at a club on one occasion in 1991. All Isle of May hatched birds older than four years recorded at clubs were on sea rocks below their natal subcolonies; where seen previously, they were attached to that subcolony. All but one were seen on the club once only. Numbers of older birds seen on clubs were so low that a χ^2 test could not be performed on the data for 1990. However, a Fisher Exact test comparing 2 and 3 year olds with 4-6 year olds was highly significant (Figure 5.2a); there was a similar significant effect of age on club visiting in 1991 (Figure 5.2b).

The seasonal distribution of visits to clubs and to the colony varied significantly in both two and three year old cohorts in 1991, club visits being concentrated earlier in the season relative to colony visits. There was no significant effect among three year olds in 1990 (Figures 5.3a-c). Sample size was inadequate in other age classes.

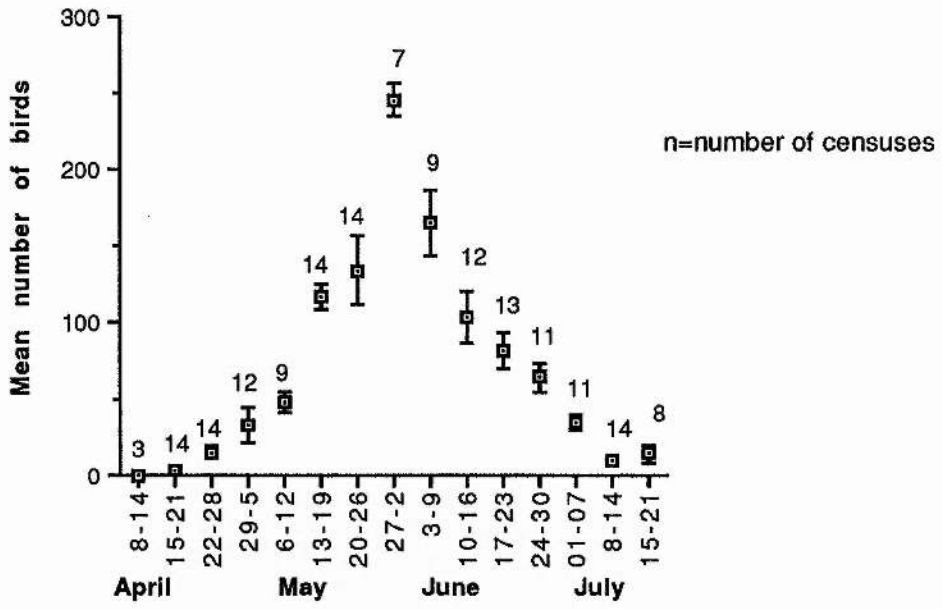
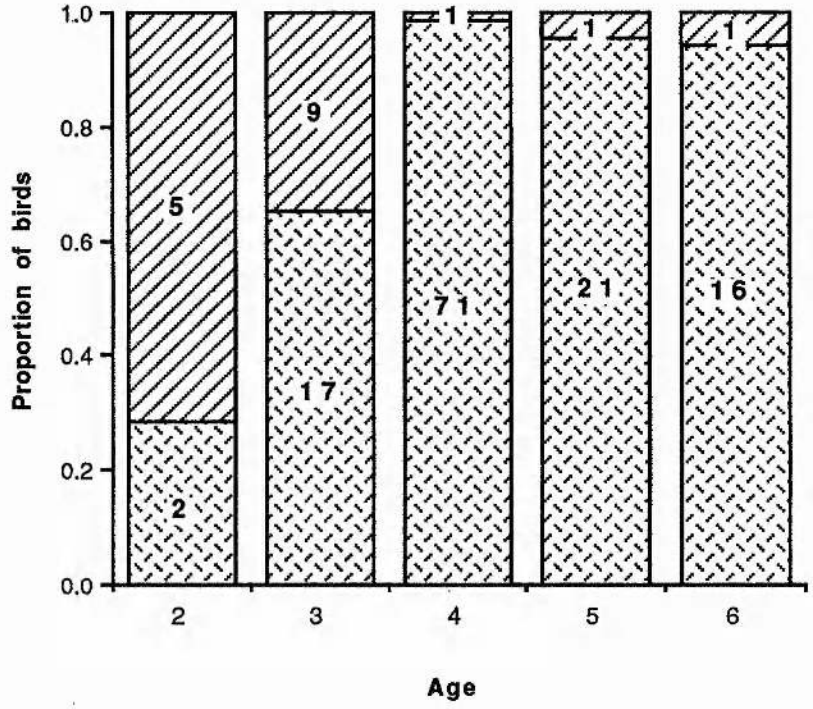


Figure 5.1 : Club attendance. Values are means ± 1SE for all censuses taken in week from twice daily censuses of focal area of colonies in 1991.

Figure 5.2a: Proportion of birds visiting clubs in 1990

Fisher Exact test
p<0.01

2-3 year old and 4-6 year old cohorts combined in calculation.

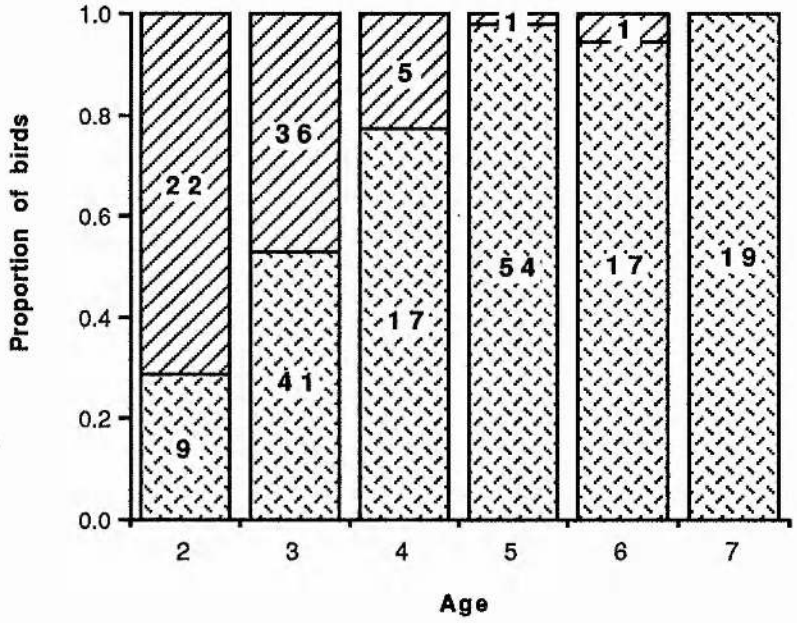


Visited club
Always on colony

n=number of birds

Figure 5.2b: Proportion of birds visiting clubs in 1991

Chi sq.=70.6,
5d.f., p<0.001



Visited club(s)
Always on colony

n=number of birds

Figure 5.3a: Seasonal distribution of location of three year olds (1987 cohort) in 1990

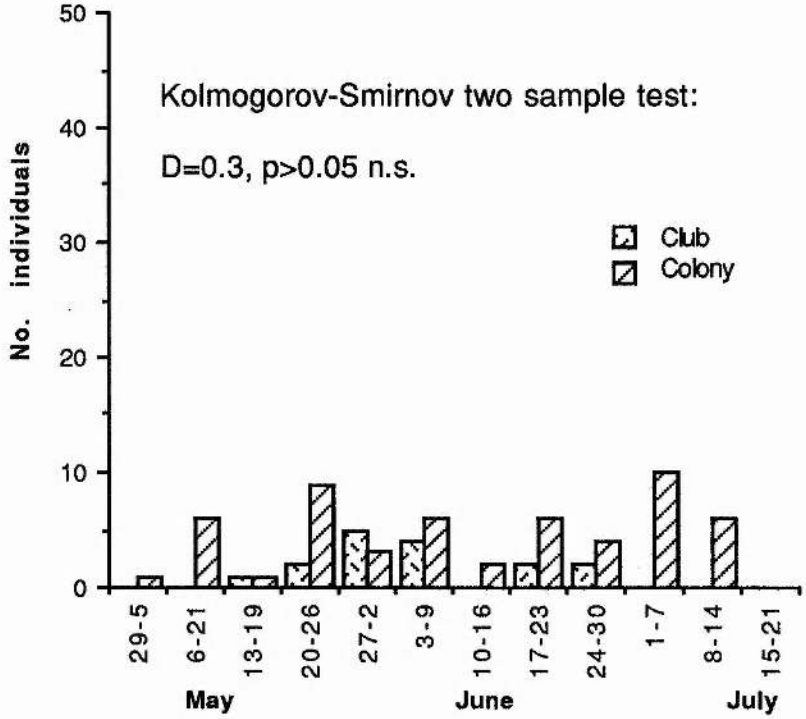


Figure 5.3b: Seasonal distribution of location of 2 year olds (1989 cohort) in 1991

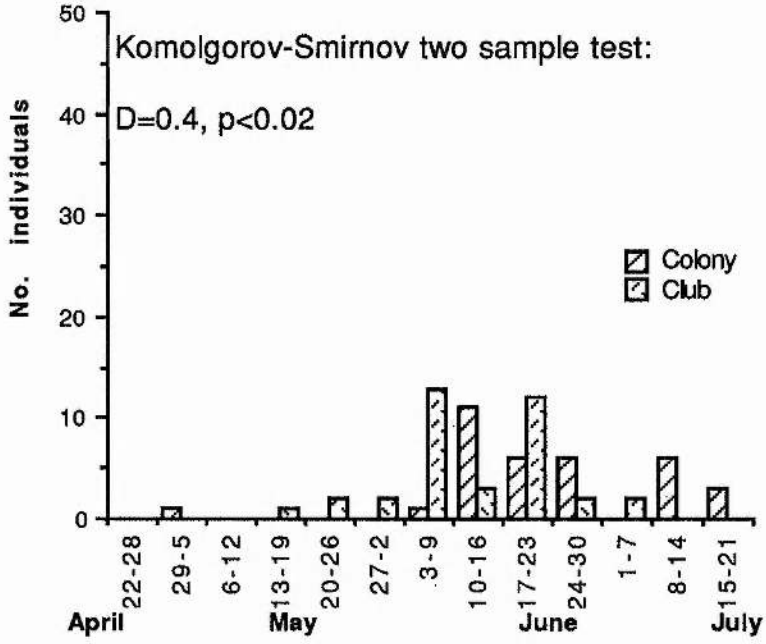
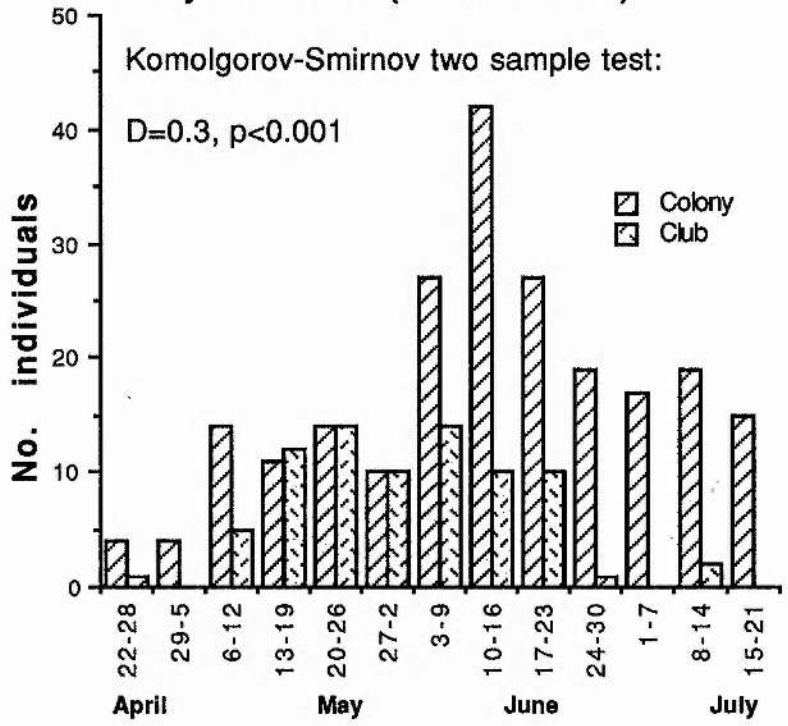


Figure 5.3c: Seasonal distribution of location of three year olds (1988 cohort) in 1991



Note that these data violate independence assumptions since the same individuals could be represented several times in the sample. (However, this is presumably true of all similar tests on age classes where individual identity is not known, e.g. Birkhead & Hudson 1977; Hudson 1979). One way of allowing for this is to observe changes in site attendance of individual birds. Unfortunately, birds in these younger age classes were, in general, observed infrequently, apparently because of lower attendance levels (Chapter 4), so that most individuals were observed only at clubs or at the colony. However, among three year olds in both seasons, sufficient individuals were seen to change the type of site they attended to permit analysis. Where a change in the course of the season from club to colony attendance or vice versa was observed, almost all did so in the direction of club to colony (Table 5.1). The effect approached significance in 1990 and was highly significant in 1991. No bird changing its attendance site from club to colony or vice versa subsequently switched back.

There was a weak trend for attachment to a particular club to be greater among 3 year olds than 2 year olds in 1991 (Figure 5.4; data were insufficient for analysis in 1990). However, this change was not significant (Fisher Exact Test, $p=0.28$). Overall, relatively few birds were attached to a particular club. Many two and three year olds were found attending more than one club, often widely separated, within a day; one three year old was seen at four separate clubs (South Horn sea rocks, Mill Door sea rocks, Rona sea rocks and Low Light sea rocks; Figures 2.2 & 2.5) at extreme ends of the island and on east and west coasts, in the same day.

5.3.2 Attendance at subcolonies

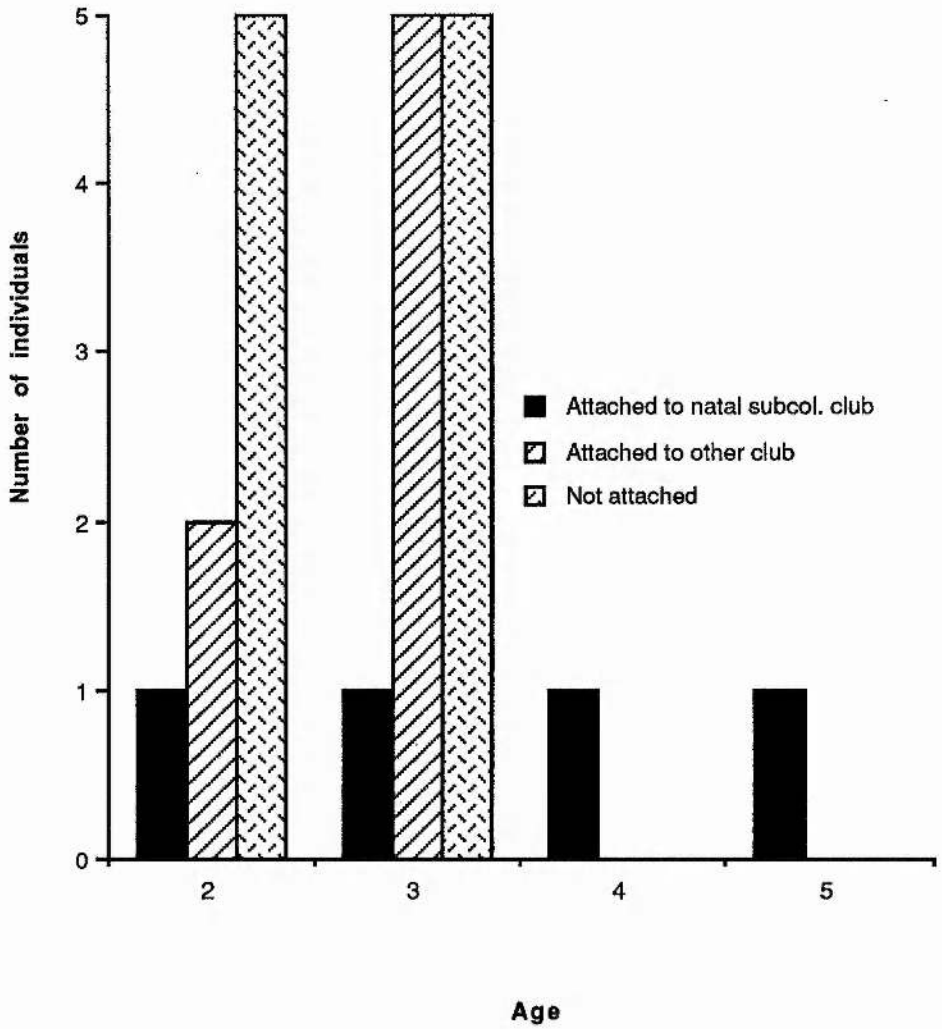
Immatures visiting cliff subcolonies where adults were breeding on Ledges or Broad ledges almost always did so at the top ledges above, and not in the body of the breeding colony itself. Birds visiting flatter sites, such as the low stacks at Mill

Table 5.1 : Individual changes in type of site attended

Year	Age	Number of birds moving from club - colony	Number of birds moving from colony - club	p[a]
1990	3	5	0	.064
1991	3	12	1	.004

[a] Binomial test

Figure 5.4: Age class and attachment to clubs among club attending birds in 1991



Door and Chatterstanes, or low density cliff subcolonies composed mainly of Single sites such as South Face, generally used nonbreeding sites and ledges within the breeding colony. Three birds which spent the 1990 season on top ledges recruited into ledge or broad ledge cliff subcolonies in 1991. All spent the previous year on top ledges above the subcolony; one began the 1991 season there (Chapter 6). This suggests that movement into the breeding colony occurs just prior to breeding on medium-high density cliff sites, presumably because sites for immatures to occupy are lacking. However, 4 birds ringed as nonbreeders on White Ledge in 1990 did move onto the Dense subcolony (directly below) in 1991, and other birds ringed on Dense, apparently as nonbreeders, in March 1991, were present there throughout the season. A problem with this data may be that most birds ringed as chicks on cliff faces are ringed near the top of the cliff, so that if birds are philopatric to their natal ledges, or prefer similar levels of the cliff to their natal sites, most known-age immatures will be seen on top ledges.

Birds at the colony were largely sedentary, rarely visiting more than one or two subcolonies. Nevertheless, the number of subcolonies visited varied significantly with age in both years (Figures 5.5a & 5.5b). Jonckeere Trend Tests, which may be used as extensions of the Kruskal-Wallis test (Cohen & Holliday 1982), indicated a significant overall declining trend with age in the number of subcolonies visited (1990: $z=2.8$, $p<0.003$; 1991: $z=2.6$, $p<0.005$). There were no differences between experienced and inexperienced birds in the number of subcolonies visited in any cohort (Mann-Whitney tests, n.s.). Fidelity to subcolonies between years was very high (92%; n=51); of the four birds which moved, three moved <50m to adjacent subcolonies.

Figure 5.5a: Mean number of subcolonies (± 1SE) visited by known-age guillemots in 1990

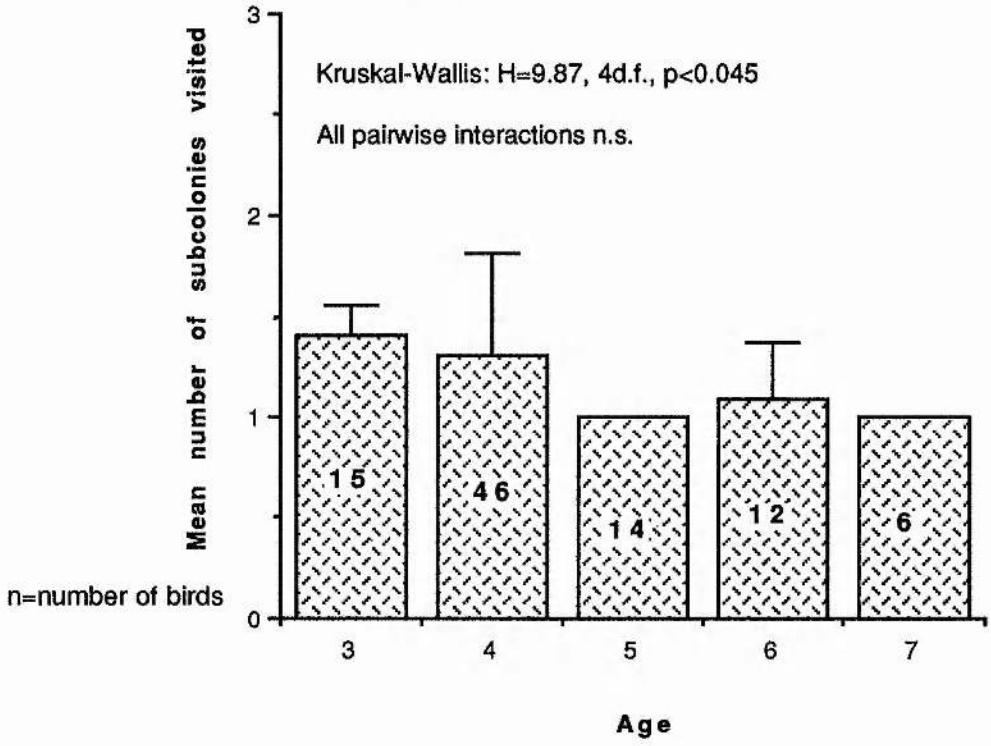
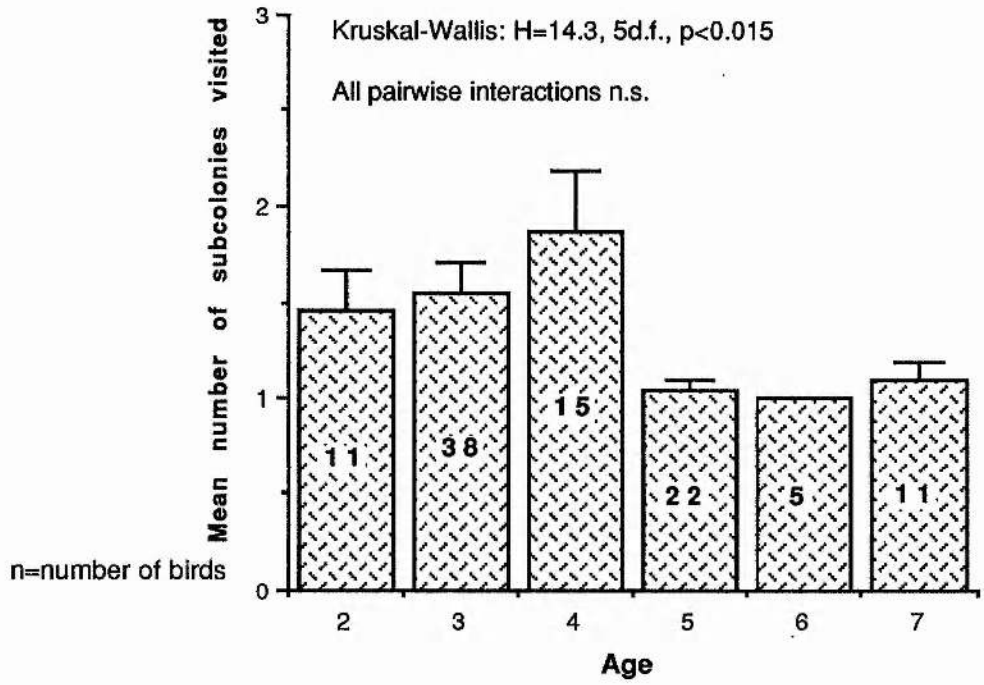


Figure 5.5b: Mean number of subcolonies (± 1SE) visited by known-age guillemots in 1991



5.3.3 Age class and philopatry

Birds were defined as philopatric if >50% of observations at colony sites were at their natal subcolony (see Methods). There was little variation with age in levels of philopatry (Figures 5.6a & 5.6b), and there was no sign that when younger birds began to attend subcolonies they were more likely to first attend subcolonies away from their natal subcolony, as compared to older cohorts, as might be expected if birds had to search to find their natal subcolonies (Figures 5.7a & 5.7b).

5.3.4 Sex and philopatry

Sexing guillemots is difficult and relies on observations of sexual interactions. As a result, relatively few immatures were sexed with certainty (Chapter 3). However, levels of philopatry did not appear to differ between the sexes. 69% (9/13) males and 73% (8/11) females were philopatric (Fisher Exact Test p=0.34 n.s.).

5.3.5 Levels of intracolonial philopatry in immatures

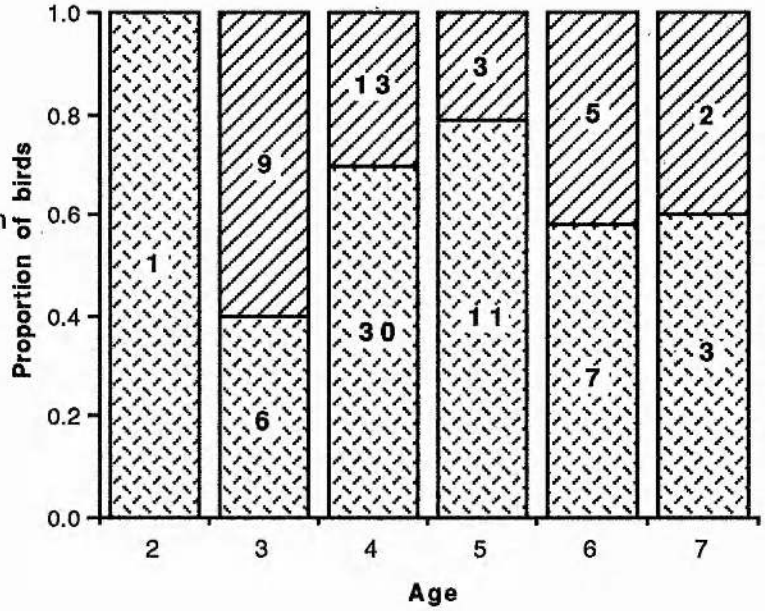
The small variations in intracolonial philopatry between cohorts do not necessarily imply that there was an influence of natality on subcolony selection. However, when tested directly, philopatry was found to be very strong in both years. Immatures had a clear tendency to select their natal subcolony as their visiting site. In 1990, 69% (67/97) of all colony-attending immatures observed were philopatric; in 1991 64% (86/134) (Tables 5.2a & 5.2b). Comparisons between actual natal subcolony attachment frequencies with those expected if birds were selecting subcolonies without a natal subcolony preference indicated a highly significant preference in both 1990 and 1991 (Figures 5.8a & 5.8b)

Figure 5.6a: Age and philopatry amongst subcolony attending birds in 1990

Chi sq.=6.15,

3d.f., p>0.1 n.s.

2-3 year old and
6-7 year old cohorts
combined in calculation



Not philopatric
Philopatric

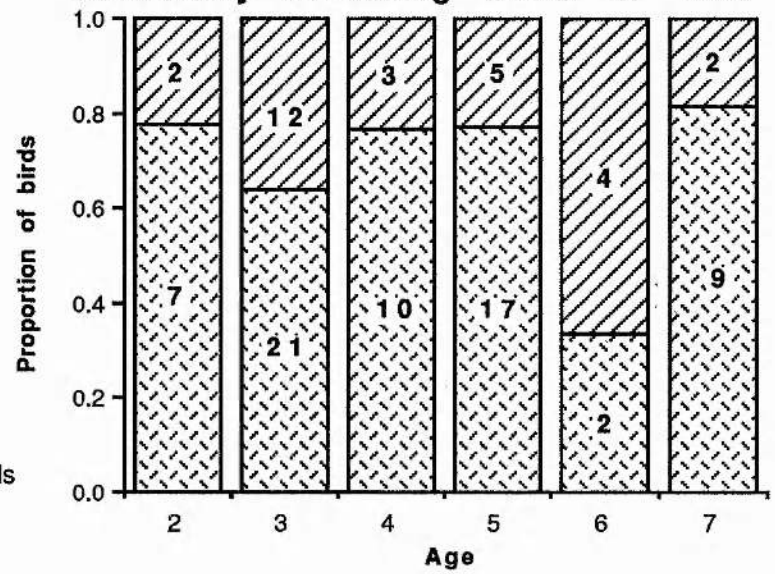
n=number of birds

Figure 5.6b: Age and philopatry amongst subcolony attending birds in 1991

Chi sq.=2.0,

4d.f. p>0.5 n.s.

6&7 year old
cohorts combined
in calculation



Not philopatric
Philopatric

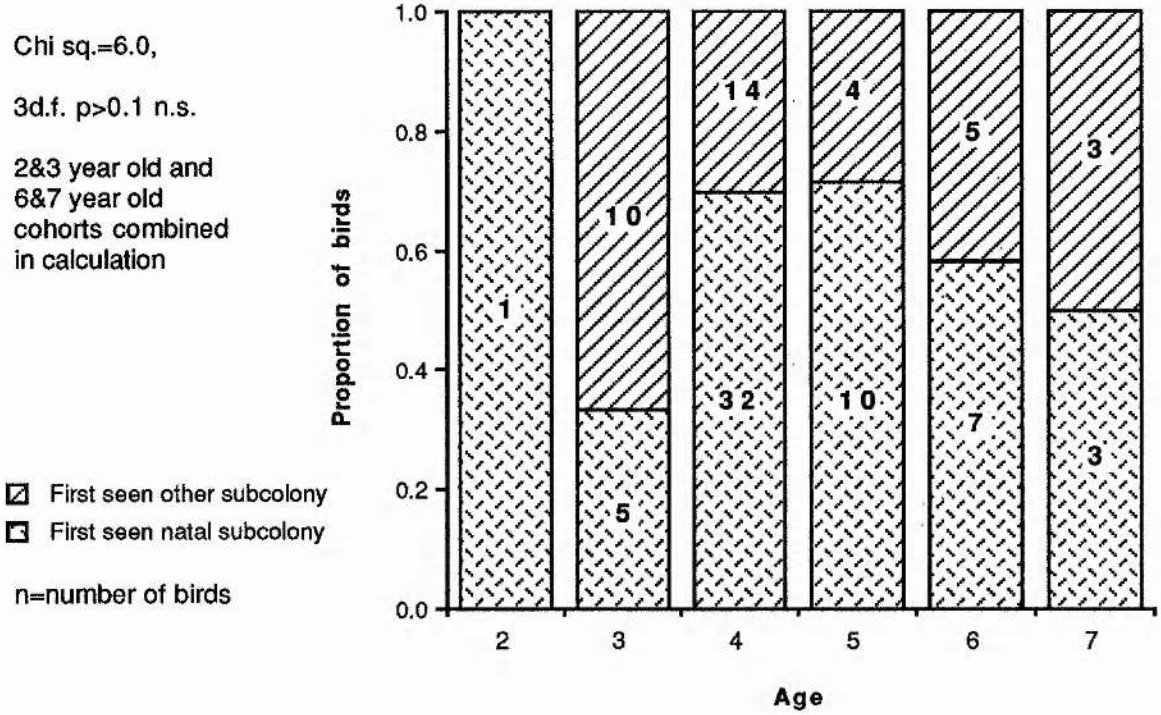
n=number of birds

Figure 5.7a: Age and first subcolony at which observed in 1990

Chi sq.=6.0,

3d.f. p>0.1 n.s.

2&3 year old and 6&7 year old cohorts combined in calculation



First seen other subcolony

First seen natal subcolony

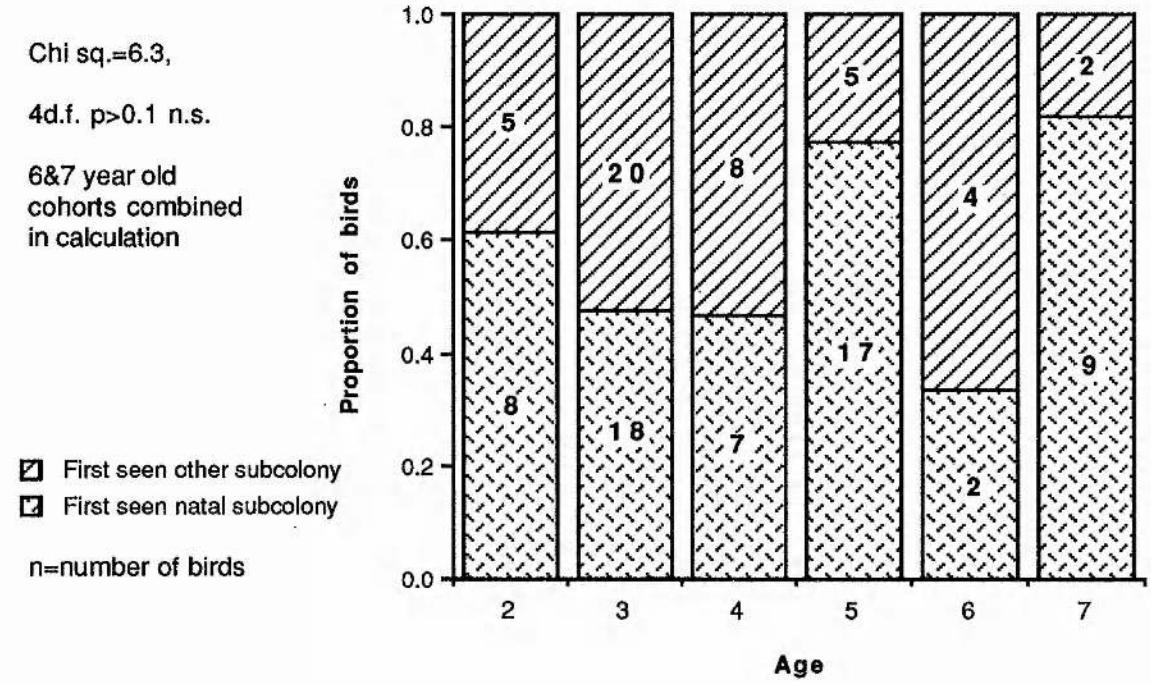
n=number of birds

Figure 5.7b: Age and first subcolony at which observed in 1991

Chi sq.=6.3,

4d.f. p>0.1 n.s.

6&7 year old cohorts combined in calculation



First seen other subcolony

First seen natal subcolony

n=number of birds

Table 5.2a: Immature philopatry in 1990

Subcolony	Number of philopatric birds attached to subcolony	Number of non-philopatric birds natal to subcolony	Total number of birds attached to subcolony[a]	Expected frequency of philopatric birds at subcolony[b]
Low Light	1	0	1	0.01
Hide	0	1	0	0
Stack	1	1	6	0.1
Colony 4	6	7	8	1.1
South Face	12	9	14	1.9
Colony B	24	6	28	8.75
South Horn	5	1	6	0.1
Mill Door	5	3	5	0.4
Rona	13	2	15	2.3
Total	**67**	**30**	**83[c]**	**14.7**

[a] Whether natal to the subcolony or to another subcolony

[b] If birds showed no preference for the natal subcolony; see methods.

[c] 14 birds were not attached to any subcolony (see methods for definition of attachment), to subcolonies where no birds natal to that subcolony were seen, or to areas of the colony where chicks were not ringed.

Table 5.2b : Immature philopatry in 1991

Subcolony	Number of philopatric birds attached to subcolony	Number of non-philopatric birds natal to subcolony	Total number of birds attached to subcolony[a]	Expected frequency of philopatric birds at subcolony[b]
Low Light	3	1	4	0.1
Stack	2	0	7	0.1
Colony 4	5	6	6	0.5
South Face	10	10	11	1.6
Colony B	26	16	32	10.0
Chatter-stanes	2	2	9	0.3
South Horn	8	3	13	1.1
Mill Door	10	3	10	1.0
Rona	20	7	23	4.6
Total	**86**	**48**	**115[c]**	**19.3**

[a] Whether natal to the subcolony or to another subcolony

[b] If birds showed no preference for the natal subcolony; see methods.

[c] 19 birds were not attached to any subcolony (see methods for definition of attachment), to subcolonies where no birds natal to the subcolony were seen, or to areas of the colony where chicks were not ringed.

Figure 5.8a: Expected and actual levels of immature intracolonial philopatry in 1990

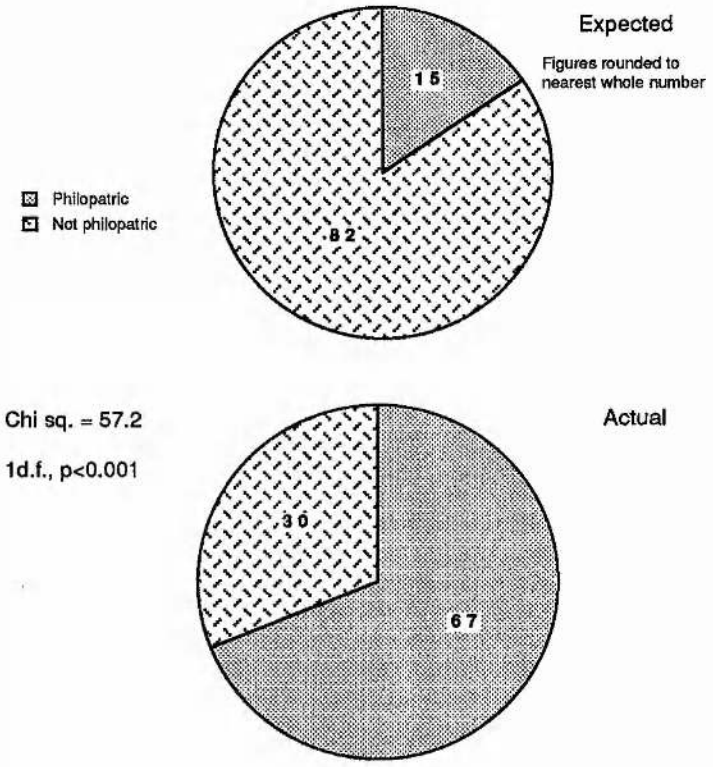
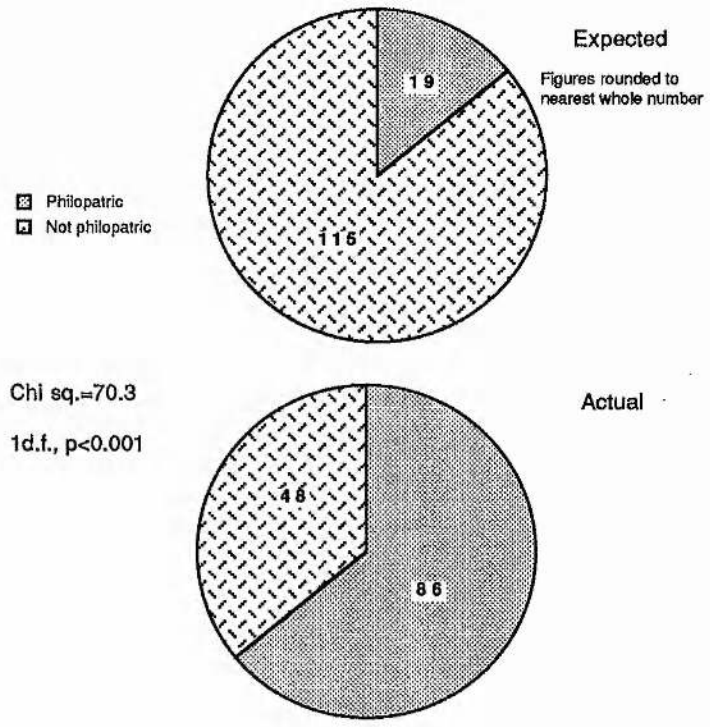


Figure 5.8b: Expected and actual levels of immature intracolonial philopatry in 1991



5.3.6 Experience and philopatry.

In most cohorts whether a bird had attended the colony in previous breeding seasons had little relation to levels of philopatry. However, an effect of experience was found for 4 year olds in 1990: philopatry was more common among experienced birds (19/21; 90%) than birds not previously recorded (15/25; 60%) (χ^2=5.5 , 1 d.f., p<0.05). Comparisons in all other age classes and in 1991 were not significant.

5.3.7 Recruitment philopatry

The preference for the natal subcolony during immaturity was followed through into recruitment. 57% of 21 birds known to have recruited in 1990 or 1991 did so at their natal subcolony (Figure 5.9). This was similar to the levels of immature philopatry measured in each year (Figure 5.10), and was significantly different from the expected level of recruitment philopatry if birds selected breeding sites without a natality influence (χ^2=8.4, 1 d.f., p<0.005; Table 5.3).

5.4 Discussion

Clubs are commonly found in colonial seabirds, especially those species where the adults are territorial. In these species immature birds congregate on the periphery of colonies, e.g. in great skuas (Klomp 1991) and gannets (Nelson 1978a). In burrow breeders immatures are generally found on the surface of the colony itself, for example in Manx shearwaters (Perrins, Harris & Britton 1973) and puffins (Harris 1983, 1984). There are variations in the composition of clubs: gannet clubs include immatures of all ages and nonbreeding birds in adult plumage (Nelson 1978a), whereas guillemot clubs are composed almost entirely of younger immatures. In all cases, clubs seem to be variable in location and levels of attendance.

Figure 5.9: Actual and expected levels of recruitment intracolonial philopatry

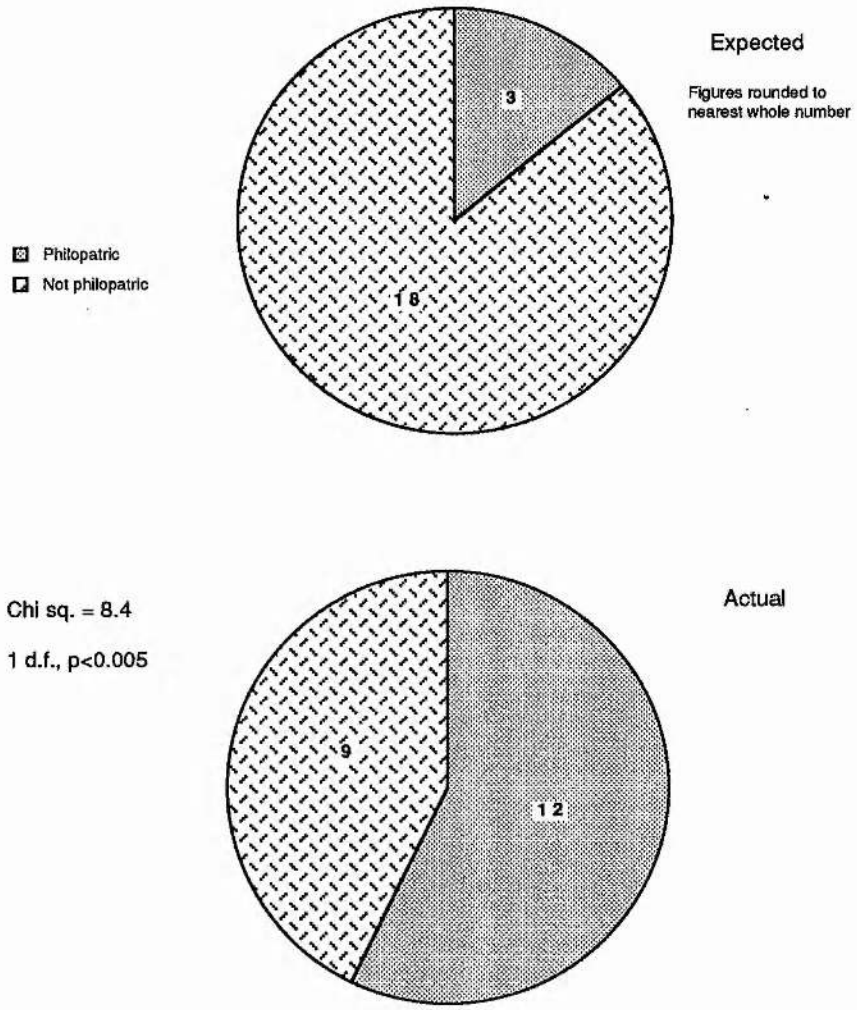


Figure 5.10: Levels of philopatry in immature and recruiting guillemots

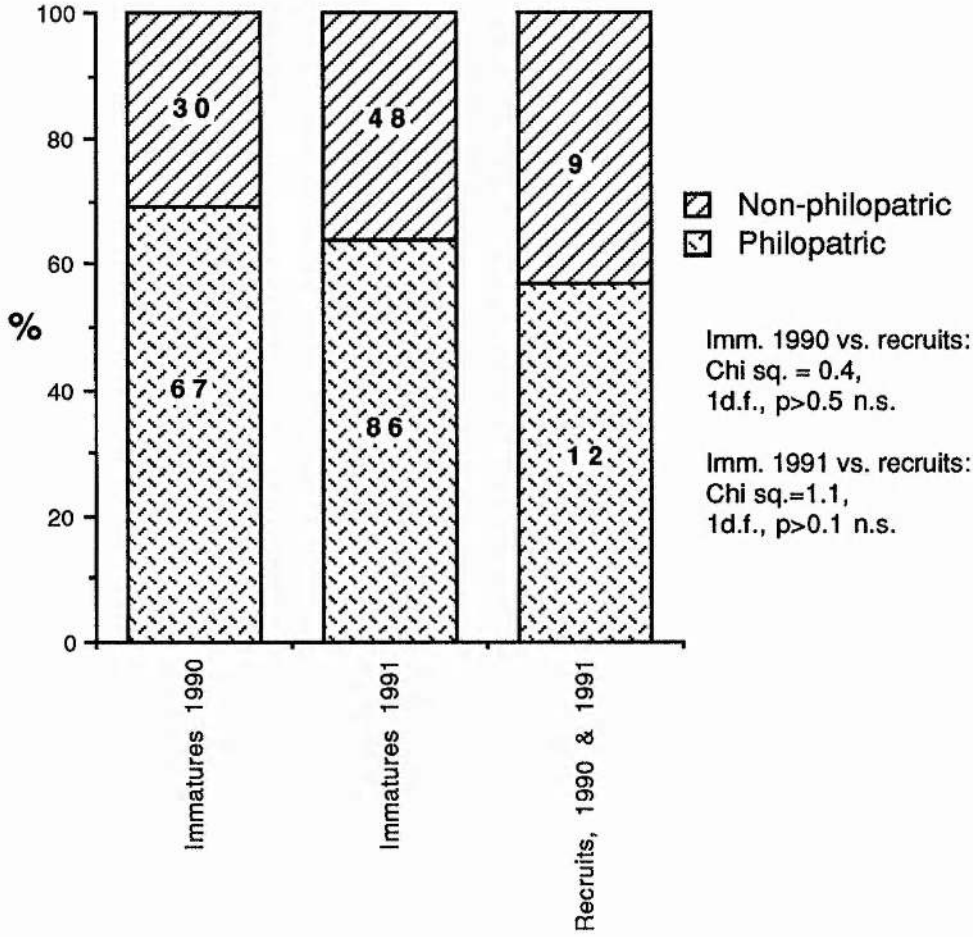


Table 5.3: Recruitment philopatry in 1990 & 1991

Subcolony	Number of birds natal to sub-colony recruiting there	Number of birds natal to sub-colony recruiting elsewhere	Total number of birds recruiting into subcolony[a]	Expected frequency of philopatric recruitment[b]
Colony 4	2	1	2	0.3
South Face	0	4	0	0
Colony B	3	3	4	1.1
South Horn	0	1	0	0
Mill Door	4	0	4	0.8
Rona	3	0	4	0.6
Total	**12**	**9**	**14[c]**	**2.8**

[a] Whether natal to the subcolony or to another subcolony

[b] If birds showed no preference for the natal subcolony; see methods.

[c] 7 birds recruited into subcolonies from which no native birds recruited at any subcolony, or to areas of the colony where chicks were not ringed.

The natural history of club guillemots on the Isle of May is similar to that of the population on Skomer (Birkhead & Hudson 1977): numbers peaking in the incubation/nestling period, and a declining trend with age in attendance, although at Skomer birds were identifiable only by age and not as individuals.

Movement from clubs to the colony later in the season was also found in the 3 year old cohort on Skomer (Birkhead & Hudson 1977; Hudson 1979). They did not find a similar effect among two year olds, as here. On Skomer two year olds were recorded on ledges on only two occasions, and for less than one minute, during four season's observations (Birkhead & Hudson 1977). On the Isle of May, two year olds were observed at colonies much more often and often seemed settled, loafing or asleep; some individuals were observed repeatedly on colonies. For example, one individual (T39808) was recorded on the colony 12 times between 29 April and 18 July, 10 of which were on the same ledge at its natal subcolony. This, together with the observation that 4 year olds were hardly ever found visiting clubs in 1990, but a minority did so in 1991, suggests that there may be behavioural differences between colonies and/or cohorts in the timing of the shift from clubs to colony.

Birkhead and Hudson (1977) attempted to estimate the age structure at clubs on Skomer from observations of cohort-marked birds (not identifiable as individuals). However, they assumed explicitly that immigration was negligible and that cohorts did not differ in detectability; neither assumption is valid in the present study. At the Isle of May a large proportion of club immatures are visitors, and their age structure differs from native immatures (Chapter 7); where individuals are not identified, the lower frequency of attendance of younger cohorts (Chapter 4) would lead to an underestimate of their prevalence in the population.

A further problem with assessing the structure of club populations where there are large numbers of immigrants is the difficulty of quantifying the proportion of the total population ringed. Birkhead & Hudson (1977) assumed in their calculation of club structure that the proportion of chicks ringed each year was similar, and within Skomer this was broadly true; however, it is not true of colonies producing the visiting birds seen on the Isle of May (Chapter 7).

Hudson (1979) suggested that guillemot clubs functioned at least partly as arenas for pairing, since birds engaged in sexual activity there more often than on colonies. However, guillemots younger than 5 years old rarely breed on the Isle of May (Chapter 6). There was no evidence that pairs on clubs were other than temporary.

Suggestions as to the function of club attendance can only be speculative; there is clearly no proximate relationship with recruitment. It seems most likely that the club serves as an initial arena for practising social and sexual behaviours. Since all Isle of May clubs were on intertidal rocks or in the splash zone, club attachment was relatively low and birds mobile. At the colony, there would be a high chance of encountering site-defending individuals; younger birds lose most agonistic interactions (Chapter 8). Club attendance would also allow birds to gain initial experience in the positioning and value of local fishing grounds relative to the colony. In addition, there are presumably few costs involved in club attendance in summer, when food is unlikely to be in short supply. Full grown guillemots have few predators at colonies.

The low number of different subcolonies visited by any individual, the decrease with age, and the fidelity between years, suggest that there is an advantage to concentrating visits at a single subcolony. Perrins*et al* (1973) also found that most immature Manx shearwaters attached rapidly to a subcolony and remained faithful thereafter. Advantages of this behaviour in guillemots may include defending a

potential breeding site, building up a pair bond, and/or gaining information on the breeding colony and monitoring opportunities for recruitment. Site defence is unlikely, since none of the birds seen in 1990 which recruited in 1991 did so at the exact site which they attended in 1990 (Chapter 6). Pairing is difficult to assess, since whether the bird was consistently paired with the same individual is unclear—in no pair were both individuals ringed. However, a ringed bird hatched in 1986 (T07709) was seen between 28 April and 14 July with a bridled bird, presumably the same individual, on a steeply sloping top ledge unsuitable for breeding. In 1991, the bird was again present with a bridled bird at the same location between 14 April and 18 July. Colony monitoring is likewise difficult to assess. There are good reasons why a bird should be selected to acquire detailed information on local breeding birds. Breeding success in some populations of guillemots is influenced strongly by the density of breeders on the ledge (Birkhead 1977). Breeding for the first time with an experienced mate enhances reproductive success in several seabird species (Davis 1976; Nelson 1966; Ollason & Dunnet 1978; Hunt 1980). Both factors suggest that there would be an advantage to immatures to get to know a subcolony, or part of a subcolony, so as to be able to take advantage of any vacancies of site or deaths of individuals. In 1991 a ringed six year old female (T07374) died between 28 June (when last seen) and 4 July (when the corpse was recovered) in the course of her second breeding season. A pair not including this bird was present on the site from at least 2 June and the site was occupied by a pair until c.14 July. This suggests that birds can be replaced very quickly after they disappear. Further, experienced birds were more likely to recruit, and did so at the subcolony they were attached to the previous year (Chapter 6). Immatures on top ledges spent much of their time looking down into the colony with neck extended, in contrast to nonbrooding adults which spent most of their time asleep or loafing facing in toward the cliff wall (Chapter 8). Taken together, this suggests that birds may attend a particular subcolony in order to be able to quickly recognise breeding or site/mate acquisition opportunities which arise.

There is little evidence that levels of intracolonial philopatry vary with age or experience. Most birds native to the Isle of May which return to the colony appear to attend their natal subcolony from the first and remain faithful to it thereafter, although birds are slightly less sedentary when younger, and in some cohorts there may be a small increase in philopatry with experience.

In most birds, including seabirds, females disperse further than males (see Greenwood 1980 for a review). It is surprising that no difference between sexes in intracolonial philopatry was detected here since presumably inbreeding risks are heightened, although birds may be able to recognise kin as in other species (Bateson 1983). It is possible that one sex has a higher tendency to emigrate outright, although the sex ratio of immatures does not support this hypothesis (Chapter 3); however, the number of birds of known sex was small.

The overall level of intracolonial philopatry is very strong. The majority of immatures and recruits which were observed were found at their natal subcolonies, far in excess of the level predicted if birds were choosing colonies without respect to natality. This result applies only to those birds which return to the Isle of May; the extent of, and any differences between subcolonies in, emigration to other colonies is unknown (Chapter 7). Differences between subcolonies in the return rate of immatures would not be reliable measures of differential emigration since, as fledging dates within subcolonies are highly synchronous (Harris & Wanless 1988), they are confounded by the apparent decline in survival rate with later fledging date in some years (Harris, Halley & Wanless *in press*).

Strictly, the data on intracolonial philopatry applies only to birds hatched at and seen on the subcolonies which were regularly checked—i.e. excluding the large subcolonies on the high cliffs between Green Face and Altarstanes. These subcolonies were very difficult to cover and were not searched on a systematic

schedule. If very large numbers of ringed chicks moved from their natal subcolonies to the high cliffs as immatures, the validity of the conclusion of philopatry might be in question. However, although eleven nonbreeders of unknown age (all but one ringed on White Ledge, close to Green Face, in previous seasons), and one former breeder from White Face, were found on the high cliffs, and a few known age immatures were seen on clubs below, no immature of known age was ever observed there. This suggests that few birds natal to the study subcolonies moved to the high cliffs, and that the population of known-age birds was philopatric.

Natal philopatry is common amongst birds and mammals (Greenwood 1980). In seabirds, intracolonial philopatry appears to be widespread. Chabrzyk & Coulson (1976) showed that 65% of herring gulls reared on the Isle of May recruited into the subcolony at which they hatched if they returned at all: some evidence suggested that most surviving birds emigrated to other colonies. Similarly, Aebischer (1985) found that shags on the Isle of May tended to recruit much closer to their natal nest than would be expected if they nested at random. Harris (1966) retrapped 268 of 303 immature Manx shearwaters on Skokholm at their natal subcolonies; Perrins, Harris & Britton (1973) estimated that 86-87% of all immatures in this population returned to their natal subcolonies. In alcids, Harris (1983) found that 87.3% of immature puffins retrapped, and the burrows of 26 of 30 recruits, were within 100m of their natal burrow. None of these studies adjusted for the "attractiveness" of different areas; however, this is unlikely to have significantly affected results. Gaston & Nettleship (1981) inferred intracolonial philopatry in Brünnich's guillemots by observing that types of egg marking (a heritable trait) were clumped. The bridled morph is also clumped within guillemot colonies (Southern & Reeve 1941). This, however, could be due to a preference for association with similar-morph birds.

Intracolonial philopatry in guillemots and other seabirds is particularly interesting because of its bearing on the functional mechanisms of natal philopatry in general. Standard explanations often include inheritance of the parental territory and its resources (Bekof 1987); adaptation to a microhabitat (e.g. Part 1991); and dangers of predation or starvation during dispersal (e.g. Murray 1967; Waser 1985). None of these are credible as explanations of guillemot intracolonial philopatry since the subcolony has no resources except the physical site itself, and birds disperse very widely outside the breeding season. By elimination, social factors would appear to be the only likely function, unless birds are imprinting on a natal area as a means of recognising the colony as a whole, with intracolonial philopatry as an accidental byproduct. Guillemots do sometimes brood one another's offspring and failed/non breeding birds may advance to attack potential nest predators, though whether these behaviours are confined to kin is unknown; breeding adults engage in mass defence by bill pointing against avian nest predators (Birkhead 1977; *pers. obs.*). While all birds gain at an individual level from this latter behaviour, additional fitness would accrue to a bird if neighbour's offspring were related to it as well. DNA fingerprinting techniques now offer a way of assessing the relatedness of breeding adults directly, but have not so far been applied to guillemots.

How birds recognise their natal subcolony is unknown. Imprinting on the natal site is a possibility, although chicks jump flightless from the cliff at c.21 days old, and on return as immatures the perspective from the air must be very different. Perhaps birds recognise kin by sight, although there is no evidence for this. Tschanz, quoted in Tschanz & Hirsbrunner-Scharf (1975) has shown that chicks learn to recognise parental calls while still in the egg. Since parents will usually be alive and resident at the subcolony when immatures return, birds may be able to cue in on parental vocalisations.

To summarise, club sites are composed mainly of two and three year old birds plus a large number of visitors hatched at other colonies. Immatures tended to move from clubs to sites in or above the breeding colonies both with age and, in native birds, as the season progressed. Populations at clubs peaked in the late incubation/early nestling period of the breeding cycle. Immatures attending subcolonies tended to do so on top ledges at dense or medium density cliff subcolonies, and on nonbreeding sites mixed in with adults at sparse cliff subcolonies and subcolonies on low stacks and rock fissures.

Immatures at subcolonies were highly sedentary, and became increasingly so as they aged. There was little difference between age classes, with experience, or between sexes in levels of intracolonial philopatry, but the overall level was high. Birds had a strong preference for attending, and recruiting into, their natal subcolonies.

Chapter 6

Recruitment

6.1 Introduction

In long lived species adult survival rates and breeding production often fluctuate little from year to year (Charnov 1986), except for occasional disasters, usually of human origin (e.g Birkhead & Hudson 1977). Guillemots in general and the Isle of May population in particular conform to this pattern (Harris & Birkhead 1985; Harris 1990). Nonetheless, changes in population occur and are commonly attributed to differences in survival and/or recruitment levels in immatures (Swann & Ramsay 1983; Harris & Wanless 1988; Harris 1990; Hatchwell & Birkhead 1991). It was demonstrated earlier (Chapter 3) that cohorts of guillemots have highly variable survival rates during the immature period. The purpose of this chapter is to investigate the rate and characteristics of recruitment in the study population, to attempt a description of recruitment in the species, to compare recruitment in guillemots to the data available for other seabirds, and to assess the evidence on recruitment levels in relation to changes in the breeding population.

6.2 Methods

Recruits are defined as birds breeding, or attempting to breed, for the first time. The minimum definition of a breeding attempt is for the bird to be a member of a pair which laid an egg. This is a somewhat narrower definition than sometimes used; e.g. Dunnet (1991) included remating "bereaved previous breeders" as recruits. However, as this thesis is concerned with the development of immature birds the

stricter criterion is appropriate. Breeders which had bred or attempted to breed in previous year(s) were termed adults.

Recruits were either birds ringed as chicks and not observed breeding in previous seasons, or birds ringed full grown in previous seasons but inferred to be immatures from low weight, poor brood patch development and/or behaviour. Every attempt was made to exclude known-age individuals whose status was unclear, but it is possible that some of these birds bred undetected in previous seasons.

Recruits were found in the course of general fieldwork (Chapter 2) and during searches of breeding ledges. Ringed birds on broad ledges in particular were difficult to find since it was often difficult to see their legs. Some were only found later in the season, and others were undoubtedly missed. After a recruit was found, its breeding progress was checked daily, except for four birds breeding on Rona or Mill Door, where checks were made every other day at a minimum. Despite this, the difficulty of obtaining adequate views of many birds meant that obtaining precise hatching and loss dates could be difficult.

Where not known exactly, a laying date was calculated from when a chick hatched, assuming an incubation period of 33 days (Harris & Birkhead 1985; Harris & Wanless 1986), unless the egg was lost. Where a date of hatching, relaying, loss of egg or chick, or leaving for the sea was not exactly known I assumed for statistical purposes that it occurred on the earlier of the possible dates, provided that the date could be narrowed to within two days. If this was not possible the record was excluded.

Recruits were sexed by observing matings, egg laying, or attendance post-fledging: successful males depart to sea with their chicks; females remain at the site (Birkhead 1976; Wanless & Harris 1986).

Breeding sites were classified into four categories according to location, density and topography (Figure 3.6).

Top Ledge sites were in areas used primarily by immatures above the main breeding ledges. Density of breeders was uniformly sparse (<3 birds/m^2) on these sites according to Birkhead's (1977) classification (Chapter 2).

Single sites were sites in the main body of the breeding colony located individually on small rock platforms or niches where birds bred out of physical contact with other pairs. Again, density of breeders was sparse (<3 birds/m^2).

Ledge sites were on rock ledges where the site was in direct contact with other sites on one or two sides, arranged linearly along the cliff face. Density of birds was medium in Birkhead's (1977) classification, >3 and <10 birds/m^2.

Broad ledge sites were on those ledges or stack tops where sites were surrounded on three or more sides by other sites. Densities were >10 birds/m^2, dense in Birkhead's (1977) classification.

6.3 Results

6.3.1 Age of first breeding

Twenty-one recruits of known age were found in 1990 or 1991. Four known-age birds had been found breeding in earlier seasons (Harris, *pers comm*) and are included here. In addition, eight individuals ringed full grown but assumed to be immatures also recruited in 1990 or 1991.

Most recruits (88%) were 5 or 6 years old (Table 6.1). The only satisfactory method of obtaining a mean age of first breeding would be to follow at least one cohort until all members had recruited. Birds of different cohorts are representatives of different sample sizes (in particular, the older cohorts are much smaller) at different stages in their life histories, and where pooled, as here, any mean will be both inaccurate and, presumably, underestimated since birds not yet recruited are not counted. The mean found for all recruits on the Isle of May was 5.44 years (±0.80 SE). One individual recruited at 3 years old in 1988 and two 7 year olds recruited in 1991. No 8 year olds recruited, although known age immatures of this age were present in very low numbers in 1991 (Chapter 3), and birds of the same cohort had recruited in earlier years at younger ages. Table 6.1 summarises information on age and recruitment.

6.3.2 Recruitment levels

Few known-age birds recruited in 1990 and 1991. The minimum figures for each cohort, birds *known* to have bred as a proportion of the number of birds in that cohort recorded that year, are given in Table 6.2. These figures are certainly underestimates. One possible method of assessing unrecorded recruitment is to

Table 6.1: Studies of the age of first breeding in guillemots

AGE OF FIRST BREEDING IN GUILLEMOTS								
Colony	Recruitment Age (Years) 2	3	4	5	6	7	8	Source
Skomer, Wales	0	0	2	1	3	-	-	Hudson 1979
Canna, Scotland	0	2	3	10	6	5[a]	-	Swann & Ramsay 1983
Stora Karlso, Sweden	0	0	0	+	?	?	-	Hedgren in Hudson 1985
Isle of May, Scotland	**0**	**1**	**0**	**13**	**9**	**2**	**0**	**This study**

[a] Aged 7 years or older (Swann & Ramsay 1983).

Table 6.2: Number and proportion of birds known to have recruited at given age in 1990 & 1991 breeding seasons.

Age and year	No. birds seen	No. recruits	% recruits
6 1990	17	1	5
5 1990	22	2	9
7 1991	19	2	10.5
6 1991	18	7	39
5 1991	55	9	16

examine the number of birds in a cohort seen. Assuming that the return rate stabilises within a cohort at ages 4 and older, and that death and emigration rates did not increase between the two years, which are plausible assumptions (Chapter 3; Chapter 7), then declines in the return rate are likely to be due to unrecorded recruitment (see discussion). The apparent return rate of both the 1985 and 1986 cohorts dropped in 1991, from 22 to 18 birds (12% to 10% of pulli ringed) in the 1985 cohort and from 72 to 55 birds (28% to 21.5%) in the 1986 cohort, suggesting there were a considerable number of unrecorded recruits.

If the decline in number of birds seen is attributed to unrecorded recruitment and added to the number of birds known to have recruited, then about 14/22 (64%) of the birds of the 1985 cohort and 26/72 (36%) of the birds of the 1986 cohort present had recruited by the end of the 1991 season. This suggests that the mean age of recruitment given above, 5.44, is an underestimate caused mainly by a combination of low survival in older cohorts, and incomplete recruitment in the younger cohorts where the sample size is more adequate. If we assume, for example, that recruitment reaches 100% in the seventh year, and that the percentages of breeding birds in a cohort are 0 before age 5, 36% at 5, 64% at 6 and 100% at 7, then the mean age of first breeding would be exactly 6 years. If some birds do not breed until older, as the data suggest, then the mean recruitment age would be even higher. These estimates, though necessarily crude given the data available, illustrate the important potential effect of unrecorded recruitment, and warn against a naive reading of recorded recruitment levels. All the data suggest that the median age of recruitment on the Isle of May is 6 years, and this is perhaps the best summary statistic to use.

The numbers of the 1985 cohort recorded on did not diminish between 1989 and 1990 (Chapter 3). This suggests that relatively fewer birds may have recruited in that cohort at 5 years old compared with the 1986 cohort (see discussion).

The population of breeding pairs fell from 12632 pairs to 11440 pairs between 1990 and 1991. With a survival rate of 91% between the years (Chapter 2), the death rate produces a figure of 22990 birds (12632 x 2 x .91) or 11495 pairs of breeding birds surviving to 1991, a figure very close to the estimated breeding population in 1991. Unless many more established breeders did not breed in 1991, the size of the breeding population could be explained without any recruitment occurring. This reintroduces the possibility that the decline in numbers of the 1985 and 1986 cohorts may have been due, at least partly, to emigration. For example, if 36% of the 1986 cohort present (3169 birds—28.1% of estimated 11275 birds fledging in 1986; see Chapter 7) recruited in 1991, this would amount to c.1141 individual recruits, or 570 pairs, and the decline in the population would be less severe than observed. Recruitment of birds from other cohorts would still further reduce the measured population decline. However, the errors inherent in measures of population and recruitment are sufficient by themselves to explain the discrepancies in population figures; a more accurate quantification of recruitment levels is clearly necessary, if difficult to obtain.

6.3.3 Sex and age of first breeding

Of the 16 recruits where sex was determined, 6 were male and 10 female (Table 6.3). Females may recruit at a younger average age as of the ten cases where both the sex and age of recruits were known all 3 males were 6 years old; 5 females were 5 years old and 2 were 6. Despite the small sample size, this difference between sexes in recruitment age approached significance (Table 6.3).

6.3.4 Experience and recruitment

Birds which recruited in 1991 arrived at the colony earlier in the season than same age (5 & 6 year old) birds which did not breed (Mann-Whitney, $p<0.001$; Figure

Table 6.3: Sex of recruits in relation to age

Sex	Age	
	5	6
Male	0	3
Female	5	2

The three year old recruit and the two seven year old recruits were not sexed. The difference in the age of recruitment between sexes approached significance (Fisher Exact Test, p=0.08).

Table 6.4: Recruitment sites in relation to age

Age	Type of site			
	Top ledge	Single site	Ledge	Broad ledge
5	6	5	0	2
6	1	4	1	1
7	0	0	1	1
?	1	7	2	0

The tendency for more five year old than older birds to recruit onto top ledge sites approached significance (Fisher Exact Test, p=0.09).

6.1). Further, 1991 recruits arrived earlier and were seen more often in the *previous* (1990) season than birds which did not subsequently recruit (Figures 6.2 & 6.3).

6.3.5 Recruitment location.

Most recruits (75%) recorded recruited to top ledges or single sites (Table 6.4). However, this could be a reflection of the difficulty of finding recruits on broad ledges. Three birds aged 5 or 6, not previously seen that year, were found holding sites on broad ledges towards the end of the season when most of the chicks and adult males had left the colony, thinning the density of birds on these ledges and allowing easier inspection of the legs for rings. These had probably bred or attempted to breed, but could not be sexed with certainty since they could have been males which had not bred successfully.

There was a suggestion of an age effect in recruitment location. Five year old birds tended to recruit to top ledge sites more than older birds. This effect was not significant, however, although it approached that level (Fisher Exact Test, $p<0.09$).

Birds apparently always recruited to the subcolony to which they were attached in previous season(s). Of 22 recruits (15 of known age) which were seen in 1990 and recruited in 1991, all bred at the subcolony at which they were observed in the former season.

Recruits also showed a significant preference for recruiting to their natal subcolony (Chapter 5).

Figure 6.1: Arrival Date (± 1SE) in relation to recruitment (5 & 6 year old cohorts) in 1991

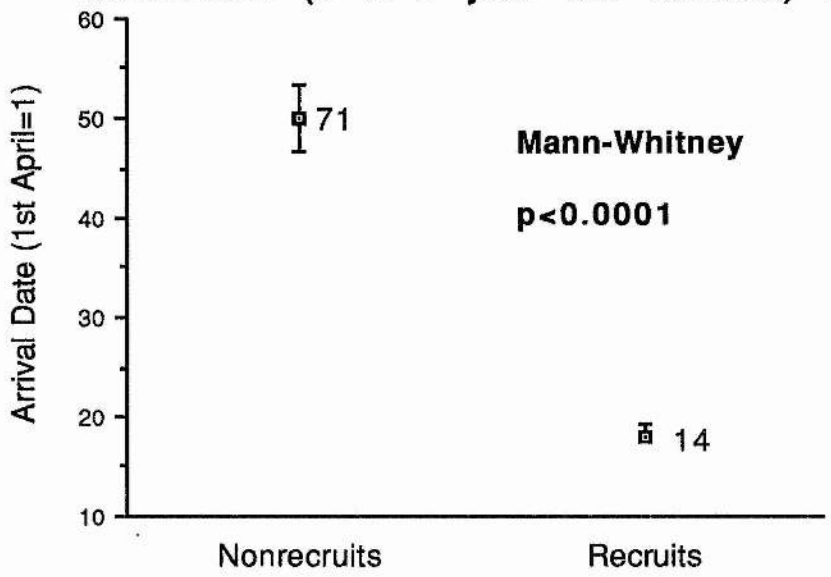


Figure 6.2: Recruitment in 1991 in relation to arrival date (± 1SE) in 1990

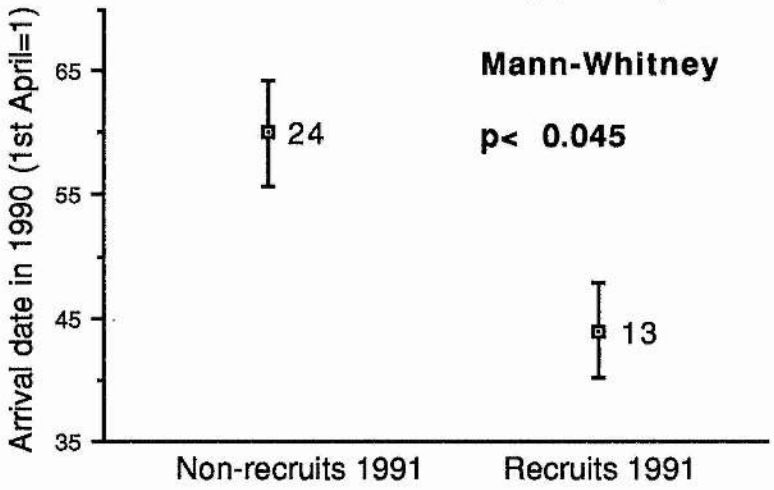
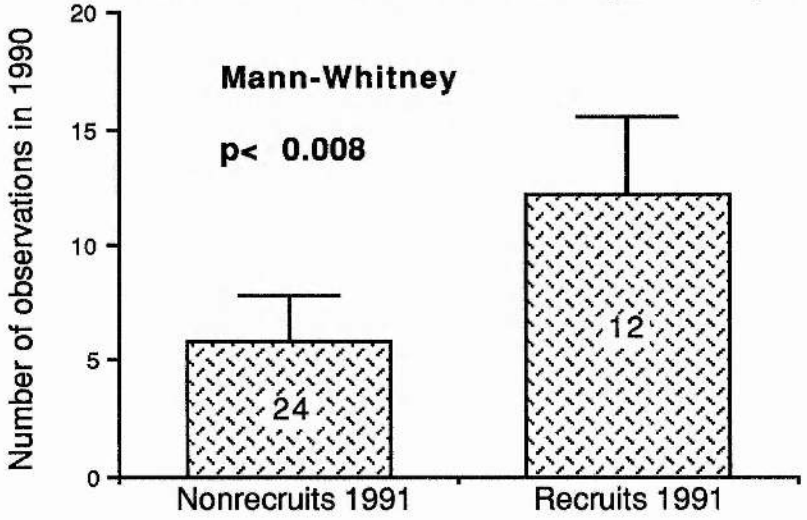


Figure 6.3 : Recruitment in 1991 in relation to number of observations (± 1SE) in 1990



6.3.6 Site acquisition

In 28 of the 29 individuals which recruited in 1990 or 1991, birds were first seen in the recruitment year at the site where they subsequently bred; in at least three cases they had secured sites, which were on adult ledges, in March, well before the breeding season commenced. In no case was the recruitment site exactly the same as the site(s) occupied by the bird in 1990 (0/22). Site acquisition was observed in only one case. The bird (a female hatched in 1986) had occupied several top ledges on the Angel stack in 1990, and regularly occupied the same ledges from 23 April to 8 May in 1991. The bird was always unpaired. On 14 May it was found, paired, on a broad ledge site among about 40 breeding pairs c.10m below. It laid on 28 May (the egg was lost on 9 June).

6.3.7 Breeding success and timing of breeding

Overall breeding success among recruits was low, 0.26 chicks fledged per pair (Table 6.5) as compared with 0.78 in 1990 and 0.81 in 1991 for the population as a whole (Harris *pers. comm.*). The median laying date was 16 May as compared with the population median of 8 May in 1990 (the 1991 date is not known). Very few birds losing eggs or chicks relaid—only one out of seventeen recruits (5.9%) which lost an egg relaid, compared with 48% in the population generally (Harris & Wanless 1988).

Breeding success among recruits appeared to be little affected by age, 5 year old recruits having a similar fledging success to 6-7 year old recruits (Table 6.5), or by type of site, top ledge and single sites not differing from ledge and broad ledge sites in fledging success (Table 6.6). Sample sizes were, however, small.

Table 6.5: Age and breeding success of recruits

Age	Stage of breeding cycle attained		
	Egg	Chick	Fledged
5	10	8	4
6	6	5	1
7	1	1	0
?	6	1	1
Total	23	15	6
%	100	65	26

There was no significant difference between 5 year olds and older recruits in the proportion of successful breeding attempts (Fisher Exact Test, p=0.24 n.s.)

Table 6.6: Type of breeding site and breeding success of recruits

Type of Site	Stage of breeding cycle attained		
	Egg	Chick	Fledged
Top Ledge	5	3	1
Single Site	11	7	3
Ledge	5	3	2
Broad Ledge	2	2	0
Total	23	15	6
%	100	65	26

There was no difference between Top ledge/sparse nests and Ledge/Broad ledge sites in the proportion of successful breeding attempts (Fisher Exact Test, p=0.38 n.s.)

6.4 Discussion

The data available on recruitment must be interpreted with care. The locations of recruits were probably biased towards birds breeding on top ledges and in low density areas of the colony, which were easier to find. Birds which attempted to breed but failed early may have been counted as immatures, and the discovery of apparent recruits holding sites on broad ledges in the post fledging period supports the conclusion that the decline in apparent numbers of the 1985 and 1986 cohorts between 1990 and 1991 may have been due to birds recruiting into the colony which were missed. However, the data on breeding populations, which suggested that population trends between 1990 and 1991 could be explained entirely by adult mortality, reintroduce the possibility that many recruitment age birds were emigrating, and that this produced the observed population decline of the 1985 and 1986 cohorts.

Further, different populations, and different cohorts of the same population, may vary in their recruitment patterns. This may have been the case with the 1985 and 1986 cohorts (6 and 5 years old in 1991). There was no decline in numbers recorded for the 1985 cohort in 1990, when it was 5 years old, in contrast to the figures for the 1986 cohort the following season. This suggests that a smaller proportion of the 1985 cohort recruited at 5 years old than was the case in the 1986 cohort. However, increases in search effort between 1989 and 1990 (Chapter 2) might have accounted for the stable numbers seen, despite unrecorded recruitment, and the 1985 cohort was relatively small.

The most satisfactory method of determining the average age of first breeding would be to follow at least one cohort from earliest to latest recruitments. Recruitment ages found in this study are extremely variable, from three years to (by inference) older than eight. The previous literature on guillemots has generally taken

the age of first breeding to be about 5 (Birkhead & Hudson 1977; Hudson 1985; Hatchwell & Birkhead 1991; Danchin *et al* 1991). This appears to rest on data from very few birds (Hudson 1979: Table 6.1); the larger sample from Swann & Ramsay (1983) indicates much the same pattern, with more very young recruits. The size and number of cohorts from which these figures were drawn are not given, so that detailed comparisons with the present study cannot be made. The present sample suggests, given that many of the birds in the cohorts studied had not yet bred at age 6, that the mean age of first breeding in the study population is in excess of six years, with a median age of 6, slightly older than the figures reported in previous studies (Table 6.1).

Variation within and between cohorts in the age of recruitment is prevalent in longer-lived birds; much evidence suggests that between-cohort variation is related to variations in social and ecological conditions (Danchin *et al* 1991 for a review). Brown pelicans reintroduced as juveniles to Louisiana, where they had recently been extirpated, bred for the first time at 3 years old, although in normal populations of the species recruitment occurs at c. 6 years old (Williams & Joanen 1974). Breeding at younger ages during a phase of population growth has also been recorded in the puffin (Harris 1981), herring gull (Duncan 1981) and guillemot (Swann & Ramsay 1983). In many species of raptor, birds very rarely breed in subadult plumage, except in populations where adult mortality is unnaturally high due to human persecution (Newton 1979). Guillemots are capable of breeding at 3 years old (Swann & Ramsay 1983; this study), and both sexes appear to be able to mate successfully at age 2 (this study) so it is likely that conditions can alter guillemot recruitment age similarly. The Isle of May population has been stable or declining recently, after a prolonged period of increase, despite roughly stable adult mortality and breeding success (Harris 1990). At the same time, feeding the young apparently became less easy for adults (Harris & Wanless 1986), although in recent years conditions have improved again (Harris 1990), which may suggest that food

supplies within foraging range of the colony were for a time relatively less abundant than formerly. A large body of evidence (Chapter 1; Burger 1990 for a review) indicates that younger birds in most seabird species are relatively deficient in foraging ability.

There are theoretical reasons why even small variations in factors such as foraging conditions, and/or social constraints such as the availability of good quality sites and the size of the surviving cohort, may affect the levels of recruitment. As Goodman (1974) has shown, in long-lived birds the payoff from reproducing must be very great (around 19 times greater depending on the exact assumptions) relative to the increased risk of mortality for reproduction to be favoured. Slight variations in conditions—for example, if the previous cohort were large and so the number of slightly older, more experienced, competitors were greater—might therefore have a strong effect on the recruitment levels of a cohort.

There is some evidence which suggests that female guillemots may recruit at a younger average age than males. Such a pattern would be in accordance with most other seabirds (Burger 1980 for a review); kittiwakes are an exception, males recruiting at younger ages than females (Aebischer & Coulson 1990). Why this should be so is unclear—the difference in kittiwakes was attributed to higher male mortality, but in guillemots no sex differences in mortality have been reported in adults (Harris & Wanless 1988; Harris 1990; Birkhead & Hudson 1977), or found in the return rates of immatures (Chapter 3). Overall parental investment is difficult to assess, but in guillemots appears to be somewhat greater in males (Wanless & Harris 1986), which should place a selection pressure on males to breed later than females, all else being equal. Males do have alternate strategies available, such as extra-pair copulations without the necessary tie to the subsequent offspring, which under certain circumstances might also tilt the balance toward a slightly later age of first breeding. Further, if female fecundity declines more rapidly than that of males,

as in many mammal species, then the cost/benefit ratio would be tilted toward earlier breeding in the female.

The salient features of recruitment age which emerge from this discussion are the variability within, and between, cohorts and the wide variety of factors which may influence recruitment age. Measures of the average age of first breeding, while useful, can serve to obscure this diversity. This is clearly a highly complex area, involving a number of constraints, costs, and benefits, at present rich in theory but poor in evidence. Closer study of the factors which do affect an individual's decision to attempt breeding is likely to be a fruitful area of research in guillemots and longer lived birds generally.

The earlier arrival of recruiting guillemots compared with same age birds is not unexpected, since only those birds arriving early in the season would be able to complete the breeding cycle. The earlier arrival and greater number of observations of subsequent recruits in the year prior to recruitment suggests that recruitment was affected by experience and/or the quality of individuals—fitter birds may have been able to spend more time at the colony as immatures and to recruit at younger ages.

The difficulty of finding birds which recruited onto ledges and broad ledges means that the percentages found recruiting to different types of site are unreliable. However, assuming that there are no biases between ages in the chances of finding a bird if it is recruited into a given type of site, cohorts can be compared. There was a suggestion that 5 year old birds may tend to recruit on to top ledge sites more often than older birds. Statistically, this result only approached significance; further evidence is required to conclusively establish the reality, or otherwise, of the effect. If the assumption is made that the effect is real, explanations for it are not easy to provide. The most obvious possibility is that the difference arises from competition for more established sites, but on the Isle of May there is no increase in

reproductive success with increasing density of breeding sites as at Skomer (Harris & Wanless 1988; Birkhead 1977). Possibly 5 year olds recruit to top ledges because they lose out in competition for experienced and/or high quality mates on established sites, as apparently occurs between "central" and "peripheral" sites in kittiwakes (Porter 1990), or that the situation on the Isle of May is unusual and the species is adapted to compete for denser sites since they normally do confer a reproductive advantage.

Birds always recruited to the subcolony they attended the previous year. This suggests that the value of prebreeding attendance may be to assess potential sites and/or breeding partners. The speed with which birds appear to acquire sites on the breeding ledges at the beginning of the season, and the abrupt transition from top ledge attendance to breeding on a site in the one case where the transition was observed, suggests that recruits are usually filling sites vacated by dead or disappeared adults. Sustained colony attendance, extreme fidelity to a single subcolony (Chapter 5), and the large proportion of time spent by top ledge attending immatures apparently observing the breeding ledges below (Chapter 8), suggest that birds develop a detailed knowledge of site geography and local breeders in a specific area of the colony so as to be able to exploit such openings as soon as they appear.

Lower breeding success and later reproduction in first time breeders is the rule in seabirds (Ryder 1980 for a review; Klomp & Furness 1991). Explanations vary from inferior foraging ability (Burger 1980), to poor pair co-ordination, possibly reinforced by (and reinforcing) hormonal imbalances (Nelson 1988), and reproductive restraint resulting in a reduced level of investment (Curio 1983). All are potential explanations of the observed pattern in the guillemot population, including the low level of relaying and the late median laying date relative to adults. Contrary to the foraging hypothesis, there was no difference between different ages

of recruit in breeding success as has been found in yellow-eyed penguins (Richdale 1957), where younger recruits bred less well, and kittiwakes (Wooler & Coulson 1977) where younger recruits bred better, apparently because birds of that age which did recruit were high quality individuals. However, the sample size in the current study was small.

In summary, what can be suggested about recruitment in guillemots from the evidence so far available seems to indicate a pattern fairly typical of seabirds: return to the natal area of the colony, and recruitment there after one or more years of prebreeding attendance. A wide spread of ages of recruitment, probably influenced by environmental conditions. Earlier recruitment, on average, of females and use of inferior sites by younger recruits. Poor breeding success.

Further work is required to follow the currently recruiting cohorts through the rest of the recruitment process and the first few years of breeding. Both the 1988 and 1989 cohorts on the Isle of May appear to be very large (Chapter 3) and offer the opportunity to study the complete recruitment process of substantial numbers of individually identifiable and known age birds over the next five years. The opportunity these birds represent to gain much more detailed information on recruitment in this species should not be missed.

Chapter 7

Intercolony movements

7.1 Introduction

Although inter-colony movements of guillemots have been noted previously (Lloyd 1980; Nature Conservancy Council 1983; Swann & Ramsay 1983), the number of records is small and guillemot colonies have often been treated as closed populations for the calculation of population dynamics (Birkhead & Hudson 1977, Hatchwell & Birkhead 1991). Recent improvements in the design of rings used on guillemots have made reading of ring numbers in the field relatively easy. Combined with mass ringing of guillemot chicks at several sites around Britain and Ireland, this has made practical the collection of data on inter-colony movements without the serious disturbance to breeding birds which would be caused by intensive retrapping. This chapter reports on the extent and nature of intercolony movements to, and as far as data permit from, the Isle of May. The implications for modelling population dynamics in the species are discussed.

7.2 Methods

Special Guillemot metal rings were introduced by the British Trust for Ornithology in 1983 (Figure 2.7). These are shaped to fit the tarsus of the bird, and present the ring number upright on both sides of the leg. Wear on the inscription is greatly reduced and readability improved compared with the previous wrap-around style of ring.

Details of chick ringing on the Isle of May are given in Chapter 2. Guillemot chicks were ringed by other workers at a number of other sites in the British Isles (Table 7.1). Except at Skomer, where most chicks were also given colour rings with a unique number combination, virtually all were ringed with BTO metal rings only. Birds seen on the Isle of May which were ringed as chicks at other colonies were termed "visitors"; birds ringed as chicks on the Isle of May and observed there were termed "natives".

Four visitors were seen on the Isle of May in 1987-89 and a further 6 were recorded in 1990. These records suggested that such visitations were a more common feature of guillemot biology than hitherto realised. Therefore, in the 1991 field season a particular effort to find, identify and describe the attendance of these birds was made. The 1991 data is used in all analyses except where otherwise noted. Five year old native birds which bred in 1991 were excluded from behavioural comparisons with visiting birds. Ringed birds were searched for in systematic surveys of the colony using 10x binoculars (Chapter 2). Ring numbers were read using 15-45x or 15-60x telescopes. In good light metal ring numbers could be read at ranges up to 100m, but normally birds could be approached much more closely. The location and type of site—tidal rocks below the breeding cliffs or on ledges within the breeding colony—on which each bird was seen was noted. Visitors were never seen at more than one type of site; a few (13) natives were seen both on sea rocks and in the colony. Where this occurred, birds were classified according to the type of site at which a majority of records were obtained.

Minimal sea distance between the natal colony and the Isle of May was calculated, assuming that birds never overflew land. Guillemots from Irish Sea colonies were assumed to travel via the English Channel, those from the Scottish west coast via Cape Wrath, as ringing recoveries suggest (Mead 1974). Data from other colonies

Table 7.1: Guillemot chicks ringed in the British Isles, 1986-89.

Colony	No. pulli ringed 1986	1987	1988	1989
Isle of May	**256**	**243**	**370**	**581**
Whinnyfold	283	701	451	303
E.Caithness[a]	1087	2031	2850	2429
Orkney	36	0	15	100
Sule Skerry	199	267	389	1
Fair Isle	1247	656	141	207
Sumburgh	1040	1201	931	733
Shiants	0	0	0	214
Canna	1912	1067	2422	2367
Sanda	3	260	498	86
Great Saltee	2017	2043	1189	2298
Skomer	251	321	299	300
Total	**8331**	**8790**	**9555**	**9619**
UK/Eire Tot.	8510	9392	10142	10265
% all chicks ringed in colonies above	**98**	**94**	**94**	**94**

[a]Includes the colonies at Ceann Ousdale, Badbea, Inverhill and An Dun.

was inadequate to assess any effect of demographic factors such as the rate of population increase/decrease on rates of colony visiting at the Isle of May.

Estimates of the populations of native and visiting immatures present on the Isle of May can be derived from figures on population and productivity (Harris 1990 and *pers. comm*; Lloyd *et al* 1991; Walsh *et al* 1991), based on the following model. The primary assumption is that ringed birds behave as unringed birds, so that the proportion of ringed birds seen directly reflects the proportion of all birds in that category that are present. This must be a minimal estimate since it assumes that no ringed birds were missed.

For a given cohort of native or visiting birds define the following terms:

Pop = size of full grown population in natal year (from counts of individual birds).

c = correction factor of 0.67 to convert counts to breeding pairs (Harris 1983).

Pr = productivity in natal year.

Rec = proportion of ringed cohort recorded on Isle of May.

Further assumptions here are that all ringed immatures visiting the Isle of May are recorded and chances of detection do not vary between classes. See below for discussion of these points.

The number of birds in the category can therefore be calculated as:

$$\mathbf{N = Pop * c * Pr * Rec}$$

Calculation for the Isle of May cohorts is straightforward as all the parameters are known for each year:

Year	Pairs breeding natal year (*Pop* * *c*)	Productivity per pair natal year(*Pr*)	Proportion cohort present in 1991 (*Rec*)	Estimated no. birds present
1986	13751	0.82	0.28	3157
1987	11680	0.76	0.11	976
1988	11223	0.85	0.21	2003
1989	12736	0.85	0.06	650

The high survival of the 1986 and 1988 cohorts are discussed elsewhere (Harris, Halley & Wanless *in press*).

Data for other colonies are much less complete. Population size is taken from the figures published for each county in Lloyd *et al* (1991); the correction factor to pairs is taken as 0.67 (Harris 1983). Thereafter a range of estimates are calculated which depend on the exact assumptions and the scale at which the data is examined:

Estimate A: The proportion of each county's cohort visiting is assumed to equal that for ringed birds from the nearest colony where ringing took place. Populations from Western Ireland, Western Isles and the English Channel excluded as there was no evidence that birds from these areas occurred. Productivity is assumed to equal that of the nearest colony for which an estimate is available (0.58 – 0.85 fledged chicks/pair: Walsh *et. al.* 1991).

Estimate B: As A. Productivity assumed at 0.8.

Estimate C: Whole British Isles population treated as a unit. Fledging success assumed at 0.8. Proportion of cohort visiting assumed to equal proportion of all ringed birds visiting.

Estimate D: As C; Western Ireland, Western Isles and English Channel populations excluded.

Estimate E: As D; productivity assumed at 0.7.

7.3 Results

7.3.1 Number and origin of visitors

A minimum of 51 guillemots not natal to the Isle of May were recorded in 1991. The complete ring number was read for 47 of these allowing them to be identified as individuals; 4 were not individually identifiable as only part of the ring number was read, but they were certainly not natives. A bird ringed as a full grown on Sule Skerry in 1986 was also seen, but its age and natal colony were not certain. Most ringed visitors originated from colonies in NE Scotland, but birds were recorded from most colonies where extensive ringing took place. The exception in 1991 was Canna, although a single 3 year old from that colony was recorded in 1989 (Figure 7.1; Table 7.1).

There was some evidence that birds natal to nearby colonies were more likely to visit the Isle of May compared to birds natal to more distant colonies. For both 3 and 4 year olds, a higher proportion of birds ringed at Whinnyfold and E. Caithness (the closest ringed colonies to the Isle of May, <350km sea distance) were observed than of birds ringed at other, more distant, colonies (3 year olds: 16/3301 (0.48%) <350km, 5/5884 (0.08%) >350km; χ^2=14.8, 1 d.f., p=0.0001.

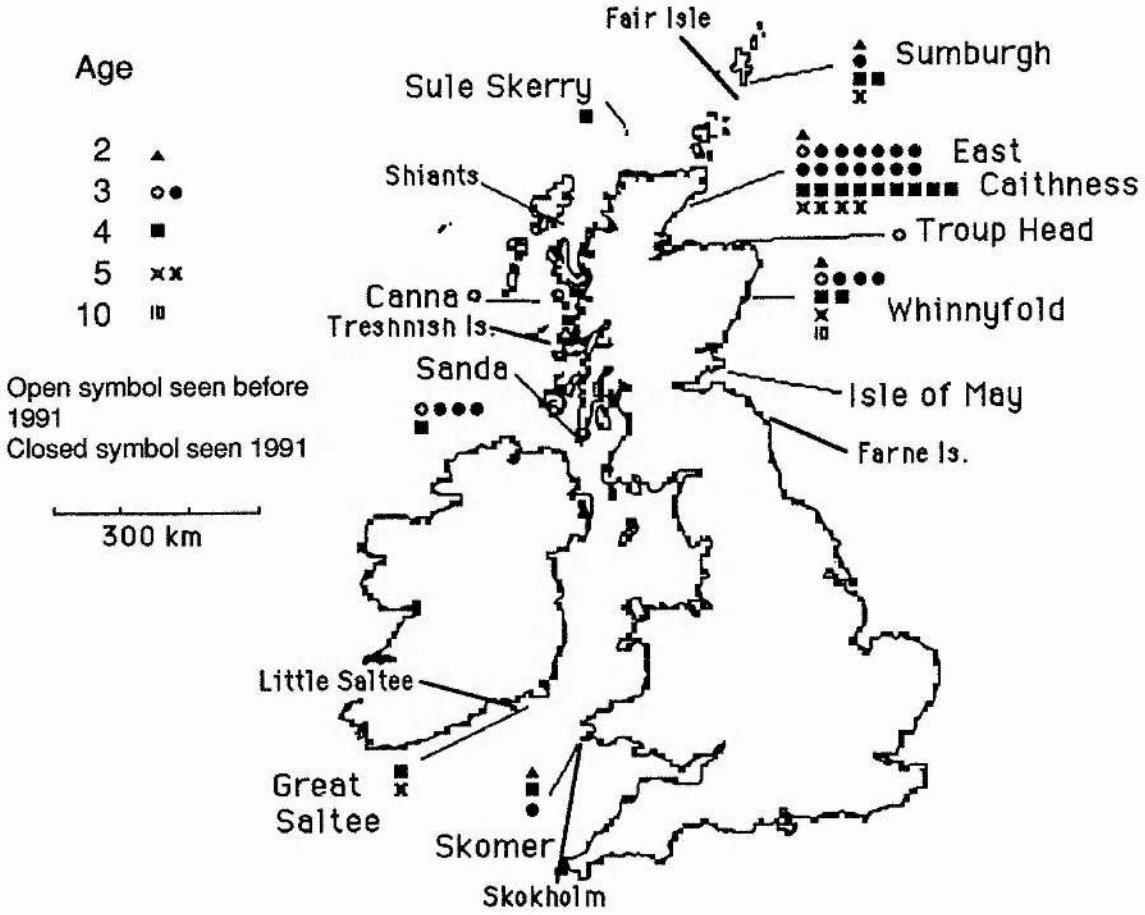


Figure 7.1: Origins of Visitors to the Isle of May

with location of other colonies mentioned in the text

4 year olds: 11/2732 (0.40%) <350km, 6/5815 (0.10%) >350km; χ^2=8.4, 1 d.f., p=0.004). Small sample sizes required combining of data into near and far categories for 3 and 4 year olds, and prevented analysis of the data for 2 and 5 year olds.

The number of ringed immatures from other colonies visiting the Isle of May varied with age (χ^2=17.4, 3 d.f., p<0.001). Relatively fewer 2 and 5 year old birds were seen than 3 and 4 year olds (Figure 7.1).

7.3.2 Isle of May birds observed elsewhere

A 1984 chick was seen on the Farne Islands, Northumberland in 1986 but was present on the Isle of May each year from 1988-91. A 1985 chick was seen on the Farne Islands in 1988, and a 1987 chick was there in 1991. A bird ringed as a chick in 1988 was observed at Sumburgh, Shetland in July 1991.

7.3.3 Behaviour

For each age class of native Isle of May birds, the number of observations of same-age birds with colour rings, and those which were not colour ringed or had lost their colour rings did not vary significantly (Chapter 3). This suggests that there was no significant bias in the probability of observation between birds with colour rings (most native birds) and birds with BTO rings only (almost all visiting birds).

Of the 51 visiting birds, 38 (74%) were seen only once, 10 (20%) twice, 2 (4%) three times and 1 (2%) on five occasions. Native birds were recorded significantly more often at all ages except for two year olds, where the sample size was small (Mann-Whitney U Tests, age 2: z=-1.6, p<0.11 n.s.; age 3: z=-3.7, p<0.0008; age 4: z=-4.01, p<0.0001; age 5: z=-2.44, p<0.015; Figure 7.2). The increase in the

Figure 7.2: Number of observations of native birds and of visitors in 1991

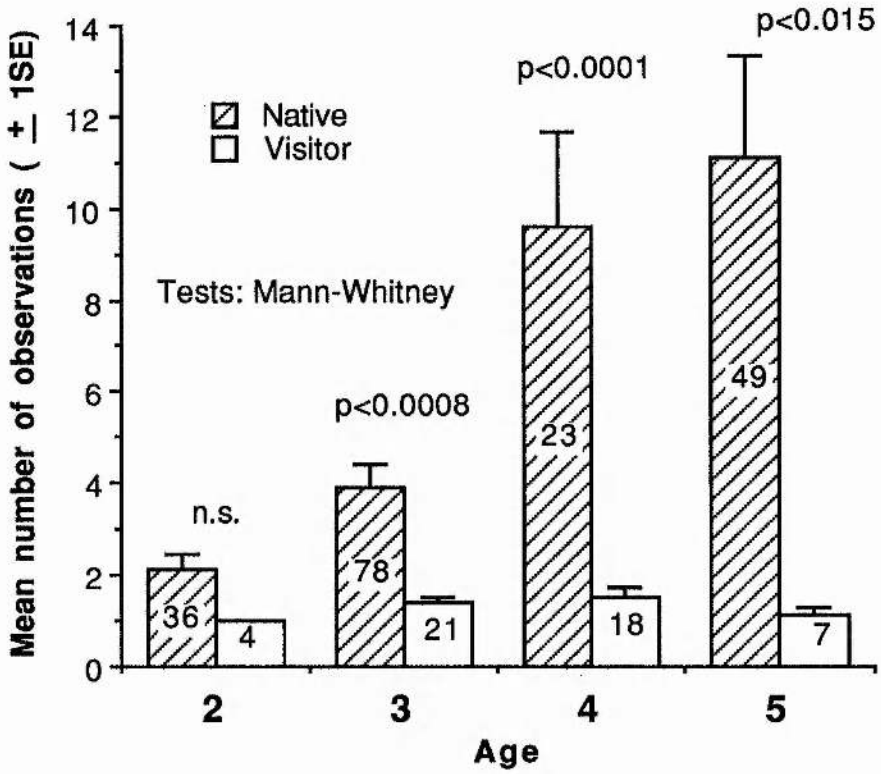
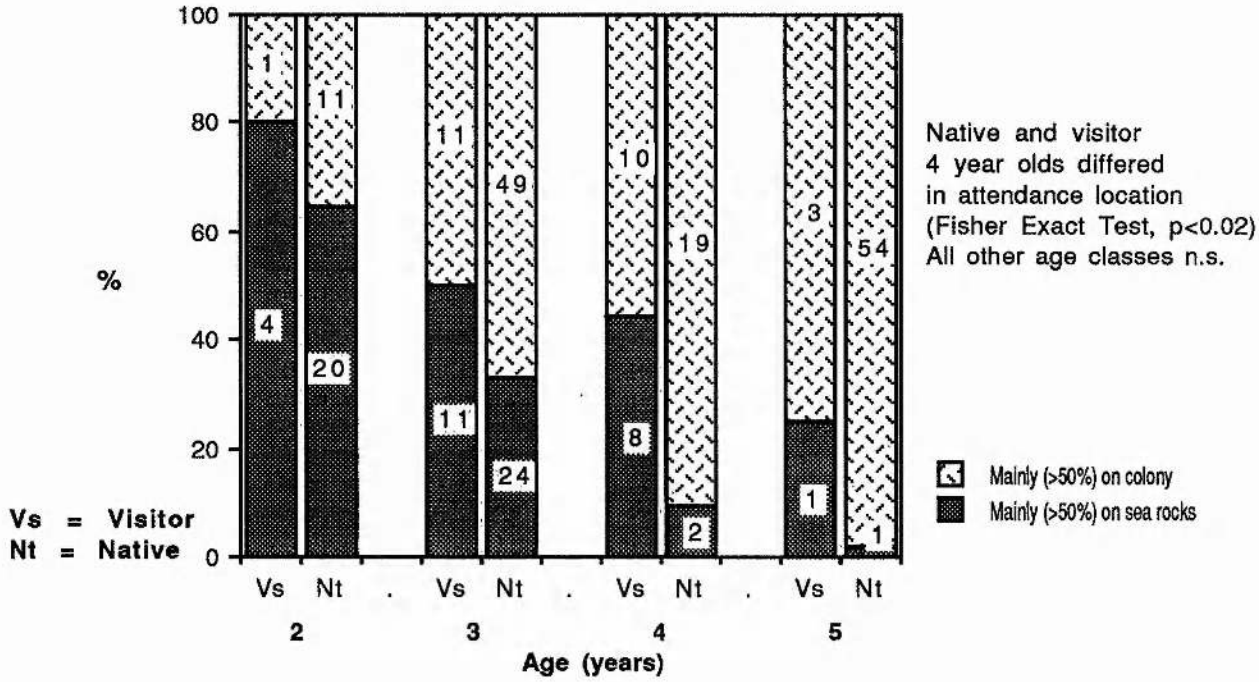


Figure 7.3: Location of native birds and immatures within the colony



number of observations with age in native immatures was highly significant (Kruskal-Wallis χ^2=20.56, 3 d.f., p<0.0001). There was no such increase in visitors (Figure 7.2).

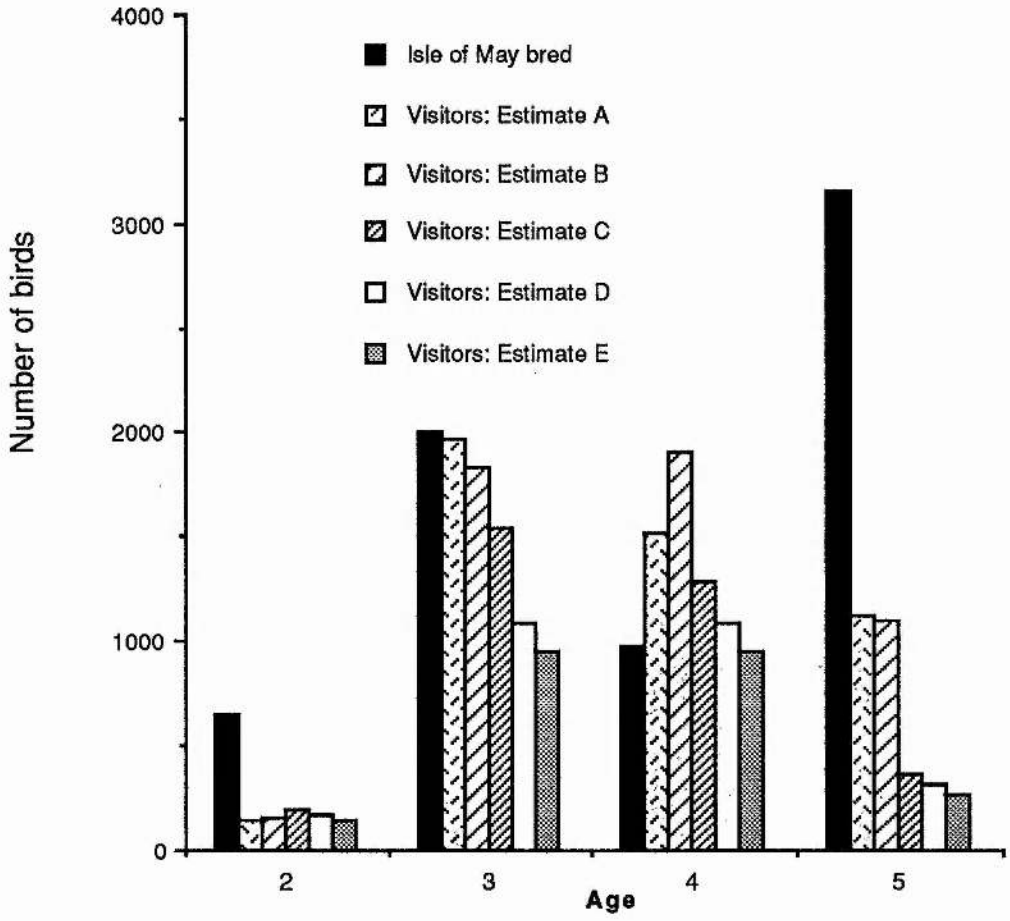
The proportion of visitors predominantly attending sea rock sites (as opposed to sites in the colony) appeared to be greater than that of natives of the same age (Figure 7.3); however, this effect was only significant for 4 year olds (Age 2: Fisher Exact Test, n.s.; age 3 χ^2=2.1, 1 d.f., n.s.; age 4: Fisher Exact Test, p=0.02; age 5: Fisher Exact Test, n.s.; Figure 7.3). The overall decline with age in the number of native birds attending sea rock sites was significant (Spearman Rank Correlation Coefficient r_s=1.0, n=4, p<0.05). For visitors the result was also significant (r_s=1.0, n=4, p<0.05), but sample sizes were small (Figure 7.3).

Two male and 2 female visitors were seen mating, in each case on sea rocks. No visiting bird in 1990 or 1991 held a breeding site or showed any indication of breeding. However, a 14 year old bird ringed as a chick on Fair Isle was seen in 1987 on 29 June at a site in the breeding colony and could well have bred and a 6 year old bird natal to Sumburgh, Shetland (c.420km sea distance from the Isle of May) bred in 1992 (Harris, *pers comm*).

7.3.4 Population sizes of native and visiting cohorts

Estimates of native and visiting bird numbers are shown in Figure 7.4. In most age classes, the models suggest that more native birds than visitors were present; however, for four of the five estimates of four year olds, visitors outnumbered native birds. Estimates of the size of the visiting population varied by up to a factor of four depending on the assumptions used in the model. These calculations assume that every ringed immature visiting the Isle of May was recorded, although a proportion were undoubtedly missed. Further, as visiting birds were seen less often

Figure 7.4 Estimates of the total numbers of native and visiting immature guillemots attending the Isle of May in 1991. A-E represent a range of estimates of the numbers of visitors present. Details of calculation methods and assumptions underlying estimates of visitor numbers are given in the Methods.


4000
3000
2000
1000
0
Number of birds
Isle of May bred
Visitors: Estimate A
Visitors: Estimate B
Visitors: Estimate C
Visitors: Estimate D
Visitors: Estimate E
2
3
4
5
Age

than natives the proportion missed was presumably higher than the proportion of native birds missed, particularly in older cohorts.

7.4 Discussion

This study demonstrates that many guillemots reared at other colonies were visiting the Isle of May and that recruitment into the breeding population did occur. The few records of Isle of May reared birds at other colonies suggest that Isle of May bred immatures were behaving in a similar way.

Previous data on inter-colony visiting by guillemots consists largely of isolated records. There were 5 sightings (not necessarily of different birds) of full grown guillemots colour dyed on Fair Isle at colonies in Shetland (NCC 1980). An immature ringed on Skomer (not necessarily a native bird) was later seen on Great Saltee (Birkhead & Hudson 1977), and Swann and Ramsay (1983) found a bird ringed as an immature on the Treshnish Isles breeding on Canna. T.R. Birkhead (*pers. comm.*) has recently recorded numbers of non-native birds (mainly from Great Saltee) on Skomer.

Inter-colony visiting has been recorded in a wide range of seabirds, e.g. herring gulls (Chabryzk & Coulson 1976), Manx shearwaters (Brooke 1978), gannets (Nelson 1978), and storm petrels *Hydrobates pelagicus* (Scott 1970). Among auks, visiting is best documented in the puffin where such movements occur throughout the species' range (Harris 1983, Kress & Nettleship 1988). In this species, immatures 2-3 years old visit several colonies before attaching to a colony and breeding. Puffin chicks ringed on the Isle of May were seen at 13 other British and Irish colonies when 4 or more years old and so were probably breeding. Almost half the surviving young bred away from their natal colony (Harris & Wanless 1991). These data refer to a colony where numbers were increasing at 19% *per*

annum, which implied that very large numbers of immigrants must also have been recruiting into the colony. Given that some young puffins seen away from their natal colony later returned to the Isle of May, colony visiting during the immature period appears to be the norm rather than the exception in this species. Inter-colony movements have also been recorded in the razorbill, black guillemot *Cepphus grylle*, and ancient murrelet *Synthliboramphus antiquus* (Lloyd & Perrins 1977, Asbirk 1979, Lloyd 1981, Gaston 1992).

On the Isle of May, few visiting guillemots were observed more than once regardless of age, in contrast to native immatures, which were observed increasingly often with increasing age. Presumably visiting birds attended the colony less often and/or for shorter periods. The type of site attended appeared to vary between natives and visitors, a greater proportion of visitors attending sea rock sites than did natives of the same age. Whether this movement from sea rocks to the colony is an effect of experience (at least at a specific colony) alone, or includes a maturational effect, is not clear.

During the study period, numbers of native birds began to recruit to the breeding population at the age of 5 years with a median age of recruitment of 6 years (Chapter 6). Fewer 2 and 5 year old visitors than 3 and 4 year olds were seen, and only 2 visitors older than 5, one of which may have been breeding, were recorded. Few native 2 year olds return to the colony, suggesting that most birds of that age remain at sea, but more native 5 year olds than younger cohorts return to the colony. Since fewer 5 than 3 or 4 year old visitors were seen, this again suggests that most visitors were not remaining to breed on the Isle of May. However, recruitment of birds from other colonies does occur, as shown by the Shetland hatched bird which bred on the Isle of May in 1992.

Attempts at modelling guillemot population structure and estimating immature survival rates have assumed that both immigration and emigration were negligible, and that colonies could be dealt with as demographically closed units (Birkhead & Hudson 1977, Hatchwell & Birkhead 1991). In the case of Birkhead & Hudson, where only the age of an immature was identifiable, the calculation of population structure depended on an assumption that each bird of every age had an equal chance of being seen. Data from this study is not consistent with these assumptions. Large numbers of non-native birds visit the Isle of May (and Skomer, the study colony for both Birkhead & Hudson (1977) and Hatchwell & Birkhead (1991); see above), and recruitment does occur. Native immatures attend the colony more often as they age, which would systematically bias the apparent population size of cohorts where they were not identifiable as individuals. Closed colony assumptions would remain valid for breeding population modelling only if very few visitors were recruited, and for population structure models if immigration and emigration cancelled out.

Non-natal colony visiting by guillemots has two potential functions, not mutually exclusive. First, and most obvious is that birds are inspecting the colony as a potential breeding site. Second, attendance may allow practice of social and sexual behaviours not possible at sea. It is also conceivable that there is no selective advantage, or risk, in non-natal colony attendance. If so, a general response to cues such as conspecific flocks and colony noise may bring a non-native bird summering or moving through the area into the colony. By analogy with puffins, it is probable that considerable numbers of guillemots do recruit into non-natal colonies. This will be difficult to prove, as it is extremely difficult to read ring numbers in the dense masses of breeding birds, but must be a priority. If recruitment occurs only rarely, the behaviour, though of interest, does not have major demographic implications. Otherwise, rates must be accurately estimated before accurate population models can be constructed for this species.

Chapter 8

Behaviour at the colony

8.1 Introduction

Immatures typically spend several years attending the colony before recruitment, and show considerable age variation in the amount of time devoted to colony attendance and the areas of the colony visited. There is, presumably, some value to attendance, and by examining what birds do while at the colony, and how this behaviour changes as birds age, it may be possible to elucidate some of these underlying factors. This chapter investigates the activity of immatures, and adults, while attending the colony. Literature on this area of seabird behaviour is relatively restricted, but data from other guillemot populations (Hudson 1979, 1985) and other seabird species (e.g. Harrington 1974, Ainley 1978, Pickering 1989) are compared and discussed with the data from this study, particularly in relation to the behavioural factors underlying deferred maturity.

8.2 Methods

Behaviour of focal birds was recorded by the continuous sampling method (Altmann 1974; Martin & Bateson 1986). Samples were of 300s in length unless the bird flew from the cliff during sampling. Where birds walked out of sight or were obscured by the movement of other birds during a sample, the sample was discarded.

Records were made on a portable Epson HX-20 microcomputer using a BASIC programme (Appendix 1) and stored on microcassette. Data were later recodified

and transferred via a BASIC translation programme (Appendix 2) into an ORACLE database and updated where further information, e.g. on the sex of the bird, had become available. Information extracted from the database via SQLPLUS programming was used in statistical tests.

Trials of the programme, behavioural categories and data collection were carried out during winter fieldwork, October 1989 -March 1990. Behavioural samples were taken throughout the fieldwork period. Intra-observer reliability was checked before each field season using videotaped behaviour samples. These tests, and further fieldwork experience, suggested that three appeasement behaviours originally included in the sampling protocol could not be reliably measured under field conditions: Stretch-away, Turn-away and Side-preening (Birkhead 1978). These behaviours were therefore subsumed into the Undefined category.

No systematic sampling schedule could be followed since recording depended on which birds were present, which could neither be controlled nor reliably predicted. Efforts were made to sample as many known individuals of as wide an age range as possible. Adults which did not have eggs or chicks were also sampled as a reference group. Adults sampled were colour-ringed individuals on single-site or narrow ledge sites (Chapter 2). Birds of known age which bred were not sampled as they formed a separate category of birds distinct from same-age nonbreeders, but were very few in number (Chapter 7). Each sample recorded the following information:

1. The Header. The following information was recorded before the beginning of the timed sample:

Identity: The ring number or (for adults) colour ring combination, each uniquely identifying the individual. Some records of unringed birds were made early in the study.

Age Class: The cohort to which the bird belonged, if immature, or status as an adult. A few birds were of unknown age class.

Sex: Where known.

Subcolony: The subcolony where the sample was taken.

Site: Site within the subcolony, where classified.

Date: Day, month, year.

Time: GMT.

Nearest Bird: The number of guillemot body lengths (excluding head) between the subject and the nearest other guillemot. 0 body lengths indicated the bird was in physical contact with another guillemot, 1 within 1 body length, etc.

2. Behaviour. Behaviour was classified into the following categories:

2a Orientation. The subject was classified as positioned:

Face out: Facing outwards from the ledge or cliff.

Not face out: Facing in toward the cliff face, away from the edge. Where the orientation of the bird was not clear cut it was classified as not face out.

Where this classification was not appropriate, e.g. on large, flat ledges, it was dropped.

2b Behaviour. The activity of the bird was divided into the following categories, only one of which could be performed at a time. The classification and suggested function of behavioural displays follows Birkhead (1976, 1978).

Alarm Bow: A stiff up and down movement of the head and neck, not involving movement of the body. Indicative of alarm or "nervousness", and contagious between groups of birds.

Alert: Defined as when the subject had its neck extended to or close to its maximum length. This normally indicated that the bird was attending to external stimuli.

Allopreening: Preening another bird. Primarily a sexual, pair-bonding behaviour (although it also occurs between incubating adults), it may also serve to reduce aggression between neighbouring birds. Allopreening usually occurred in bouts where birds alternated with their partner in allopreening. Both allopreening and being allopreened have been scored together. The identity of the partner was recorded.

Bowing: A downward movement of the whole body, the bill frequently touching the ground between the bird's feet. A 'one-sided' version of the Mutual Bow (below) and apparently a site-ownership display.

Mutual Bowing: Occurs almost exclusively between paired birds. Synchronised bowing, the birds often bill-fencing at the bottom of the bow and allopreening. Apparently primarily a site-ownership display, probably with a secondary function of reinforcing the pair bond.

Fish Presentation: The bird holds a fish lengthwise in its bill, usually with neck outstretched, and may engage in bowing. The fish may be brought back by either sex (Halley 1986) although earlier accounts (Birkhead 1976) considered that only females returned with fish. Where pairs engaged in fish presentation, the fish was frequently passed between the birds. The function, however, appears primarily to be a site ownership display (Halley 1986).

Fight: An escalated level of aggression. Fighting birds grappled and bit, attempting to maintain contact with their opponent and shaking him/her. cf. Jab, below. The identity of the opponent, where known, was recorded, as was the initiator of the fight and the winner. Where no bird was clearly the victor (by, for example, displacing the opponent or receiving an appeasement display) the fight was scored as a draw.

Jab: Pecking at and/or being pecked by an opponent, bill closed. The opponent, initiator and winner were noted as for fights (above).

Neck Point: A threat display. The subject points bill, head and neck outstretched, at the opponent in a stereotyped manner, often accompanied by semi-open wings and standing on feet rather than feet and tarsi, increasing apparent size. Often followed by an escalation to jabbing, or by an appeasement display by the opponent. Opponent, initiator and winner noted as for fight.

Ritual Walk: An appeasement display used when moving between or close to other birds. Moving between birds, the neck is stretched and the head pointed up; close to birds (such as at the edge of a ledge) head and neck point down. In both cases, the wings are usually held out behind the bird.

Mate: Mounting or attempting to mount, or being mounted by, another bird, whether or not cloacal contact occurred.

Pebble Carry: The subject holds a small pebble, piece of vegetation, or feather in its bill. The function is not clear, but may be similar to Fish Presentation (above).

Undefined: All periods in which none of the above behaviours occurred. Most time classified into this category was spent loafing, sleeping or preening. Some behaviours rare in immatures, such as greeting displays, and those which could not be reliably recorded, such as Stretch Away, Turn Away and Side Preening, were included.

Error: indicated that the previous keypress was erroneous. The cause of the error was noted after the sample was collected and rectified during the data-cleaning process after loading into the database.

With this design of data collection, two separate streams of behaviour, orientation and type of behaviour, were measured concurrently. The translation program (Appendix 2) calculated the length of bouts for the behaviours in each behavioural stream separately. Individual alarm bows were very brief, usually <1s, the shortest time period which the recording programme could distinguish. For this behaviour, therefore, the number of bows rather than the amount of time spent alarm bowing was used in statistical tests.

Many birds were sampled more than once in the course of a season. Where this occurred, the mean score for the bird was used in comparisons between age classes (Machlis *et al* 1985). For comparisons between years, a within-subjects or matched pair approach was used, comparing the scores (or mean scores where more than one sample was taken in a year) of individuals sampled in both years.

Where a behaviour was sufficiently common, differences in the amount of time spent engaged in the behaviour between age classes were analysed using Kruskal-Wallis one-way analysis of variance. For rarer behaviours, birds were classified by whether they performed the behaviour or not and a χ^2 or Fisher Exact test performed on the resulting matrix. In order to prevent possible biases arising if birds in different age classes were sampled a different number of times on average, where a bird was sampled more than once in a year the sample from which data were extracted was chosen at random. Comparisons between years used mean scores from all samples of an individual in each year in a Wilcoxon matched-subject test.

8.3 Results

8.3.1 Number of samples

513 behavioural samples were taken in 1990 and 415 in 1991. The number of individuals of each age class sampled in each year is shown in Table 8.1.

8.3.2 Proximity to other birds

There were overall significant differences between age classes in average proximity to other birds in both 1990 and 1991. Post-hoc testing showed that adults tended to have a significantly shorter nearest-neighbour distance than birds of the 1986 cohort in 1990, and a shorter nearest-neighbour distance than all other age classes except the oldest, 1984-85, immature cohort in 1991. The 1984-85 cohorts had a significantly shorter nearest-neighbour distance than the 1988 cohort in 1991. If adults were excluded from the analysis, the 1984-85 cohorts had a significantly shorter nearest neighbour distance than each of the 1987, 1988 and 1989 cohorts in 1991 (Figures 8.1a & 8.1b).

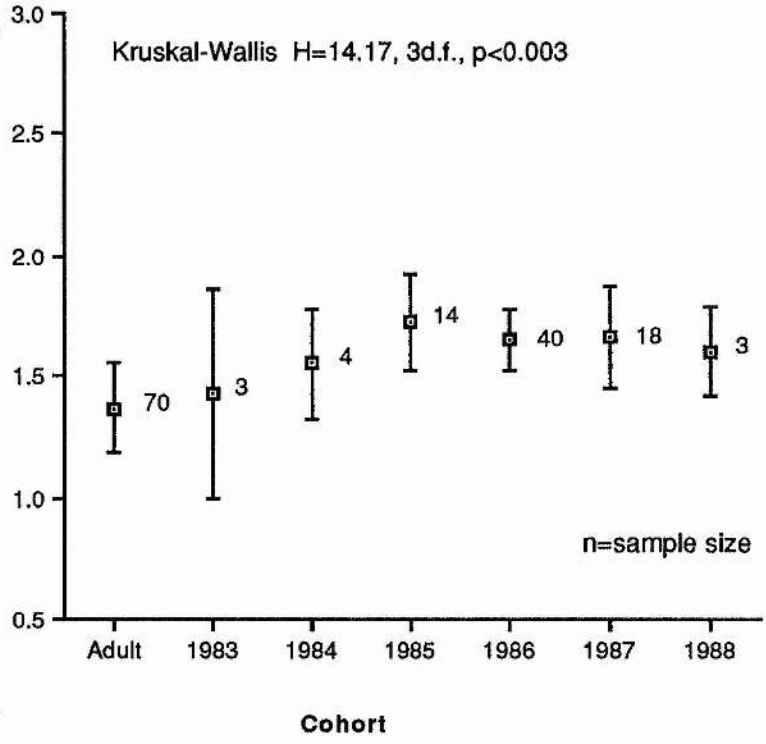
Table 8.1: Number of individuals in each age class sampled in 1990 and 1991.

Age Class	No. individuals sampled 1990	No. individuals sampled 1991
Adult	69	75
1983	3	0
1984	4	4
1985	14	12
1986	40	35
1987	17	19
1988	3	27
1989	0	11
Immature[a]	0	9
Other[b]	19	3

[a] Birds of unknown age but which were not breeding in the current season and had not previously bred.

[b] Birds of unknown status, unringed birds, age class ringed birds which subsequently bred in that season, and previous breeders without mates or sites in the current season. The figure is a minimum since the number of unringed individuals sampled was not known.

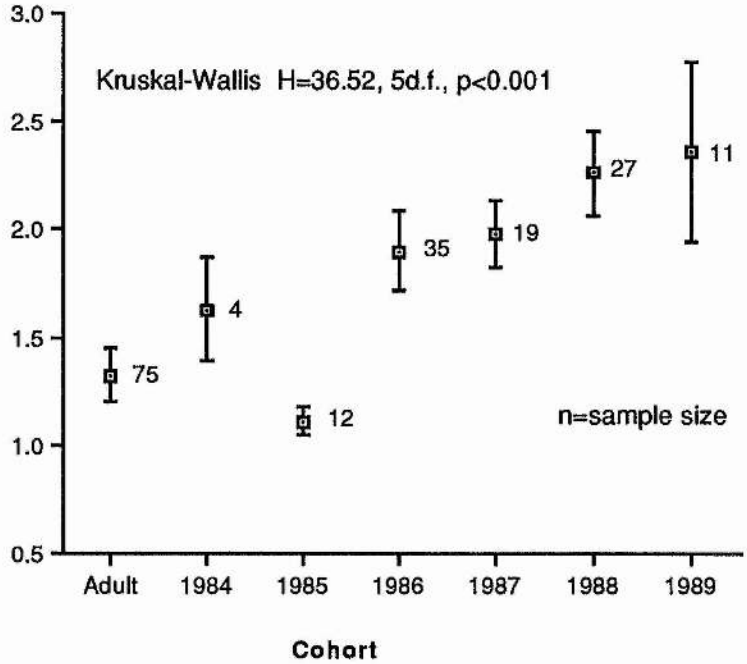
Figure 8.1a: Mean proximity (± 1SE) of birds of known age to the nearest bird in 1990



1983-85, 87-88 cohorts combined in calculation

Multiple-comparisons posthocs: Adults vs. 1986 cohort significant, $p<0.05$. All other pairwise comparisons n.s.

Figure 8.1b: Mean proximity (± 1SE) of birds of known age to the nearest bird in 1991



1984-85 cohorts combined in calculation

Multiple-comparisons posthocs: Adults vs. 1986, 1987, 1988, 1989 cohorts significant, $p<0.05$. 1984-85 vs. 1988 cohorts significant. All other pairwise comparisons n.s.

8.3.3 Orientation

Adults spent much less time facing out than all immature cohorts in both years, but immature cohorts varied little in the amount of time spent facing out (Figures 8.2a & 8.2b). Post-hoc testing showed significant differences between adults and all other age classes in both years, except for the 1989 cohort in 1991, where the sample size (11) was small. This result reflected the adult tendency to stand or sit on the breeding site facing in towards the rocks, immature birds being much more variable in orientation.

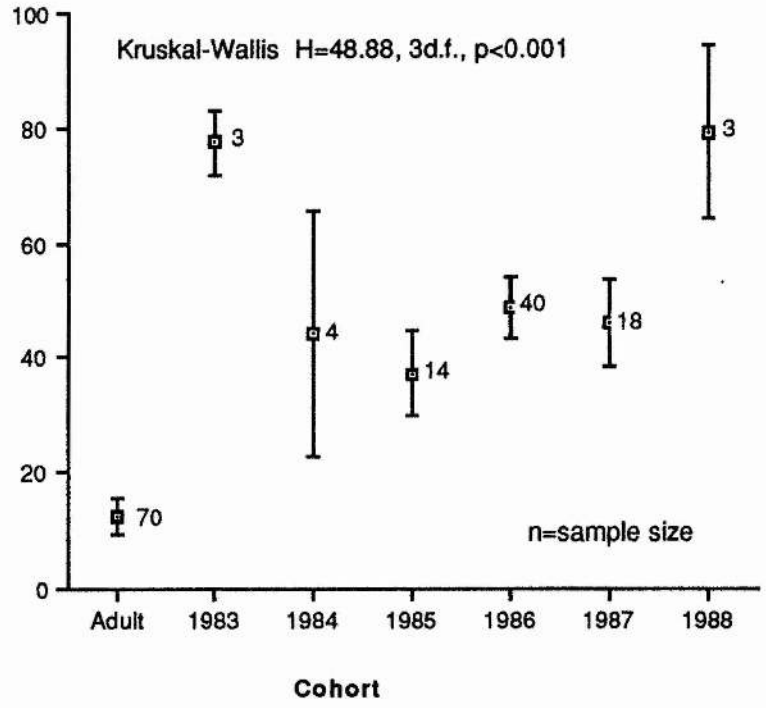
8.3.4 Alert posture

Adults spent much less time alert than immatures, which varied little between cohorts in the amount of time spent alert. Multiple comparisons post-hoc tests showed significant differences between adults and all other age classes in both years, but no pairwise comparisons between any immature cohorts were significant (Figures 8.3a & 8.3b).

8.3.5 Allopreening

Adults spent more time allopreening than immatures of all age classes in 1990; multiple comparisons post-hoc testing found significant differences between adults and all other age classes in 1990 (Figure 8.4a). There was no apparent overall pattern related to age in 1991 and no pairwise comparisons were significant; however, there was an overall significant difference between age classes in allopreening (Figure 8.4b). Although there were no significant pairwise comparisons, multiple comparisons posthocs indicated a significant difference between the high levels of allopreening in the 1984-85 cohorts (combined for

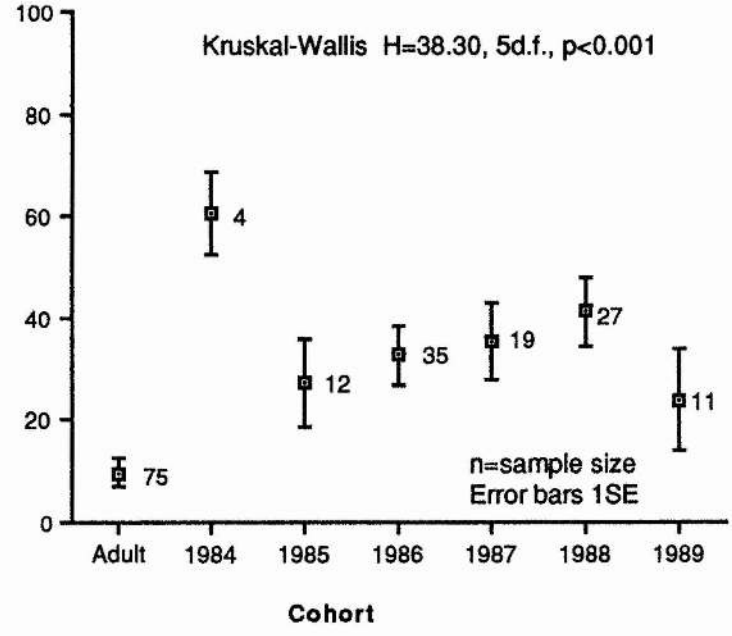
Figure 8.2a: Mean proportion of time (± 1SE) spent Face Out by birds of known age in 1990



1983-85, 87-88 cohorts combined in calculation

Multiple-comparisons posthocs: Adults vs. all other cohorts significant, $p<0.05$. All other pairwise comparisons n.s.

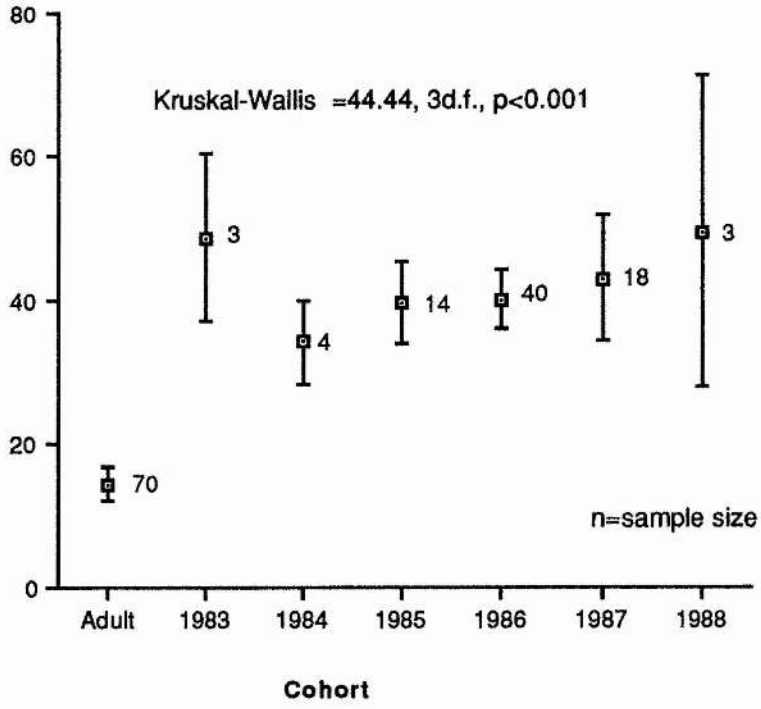
Figure 8.2b: Mean proportion of time (± 1SE) spent Face Out by birds of known age in 1991



1984-85 cohorts combined in calculation

Multiple-comparisons posthocs: Adults vs. all other cohorts except 1989 significant, $p<0.05$. All other pairwise comparisons n.s.

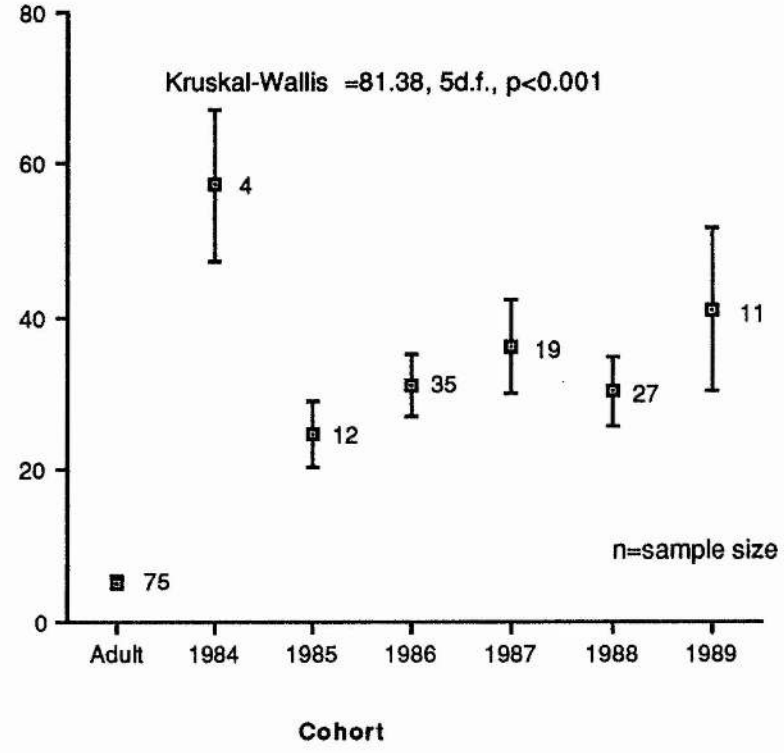
Figure 8.3a: Mean proportion of time (± 1SE) spent Alert by birds of known age in 1990



1983-85, 1987-88 cohorts combined in calculation.

Multiple-comparisons posthocs: Adults vs. all other cohorts significant, p<0.05. All other pairwise comparisons n.s.

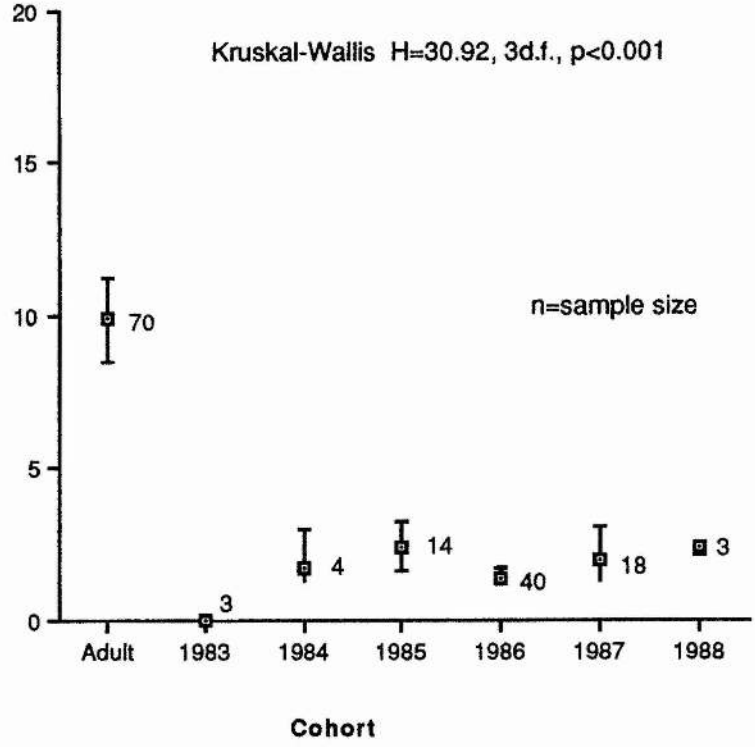
Figure 8.3b: Mean proportion of time (± 1SE) spent Alert by birds of known age in 1991



1984-85 cohorts combined in calculation.

Multiple-comparisons posthocs: Adults vs. all other cohorts significant, p<0.05. All other pairwise comparisons n.s.

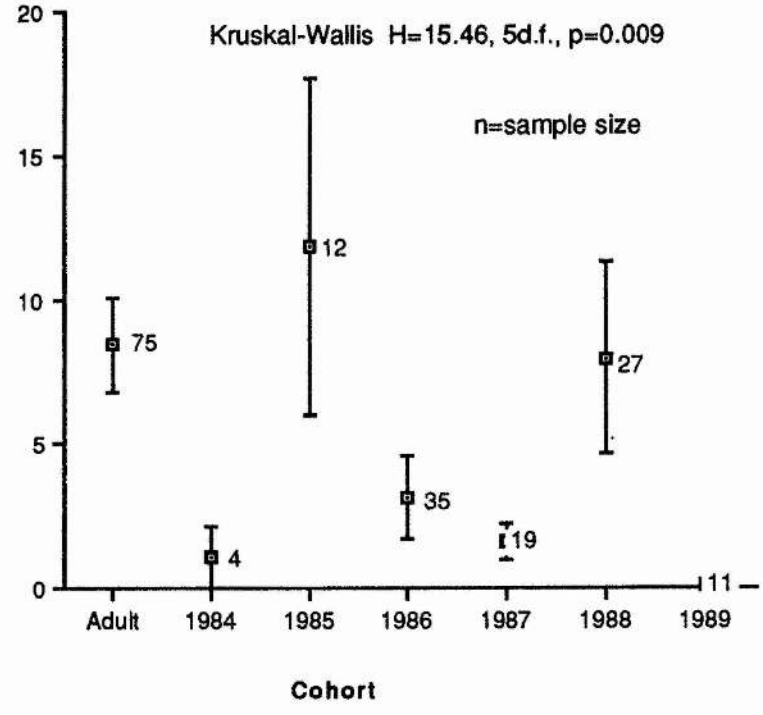
Figure 8.4a: Mean proportion of time (± 1SE) spent Allopreening by birds of known age in 1990



1983-85, 87-88 cohorts combined in calculation

Multiple-comparisons posthocs: Adults vs. all other cohorts significant, p<0.05. All other pairwise comparisons n.s.

Figure 8.4b: Mean proportion of time (± 1SE) spent Allopreening by birds of known age in 19



1984-85 cohorts combined in calculation

All pairwise comparisons n.s.

calculation purposes) and the 1989 cohort if the adult age class was excluded from the calculation.

Data were collected on the identity of allopreening partners; however, for almost all immatures the partner was an unringed bird of unknown age and breeding status. A 1986 bird allopreened another 1986 bird and two immatures of unknown age allopreened one another. Adults allopreened their mates or occupants of adjacent sites.

8.3.6 Bowing

Bowing varied rather little between age classes, and although adults and older cohorts did seem to engage in bowing more than younger age classes in 1990, there was no significant effect in either year (Kruskal Wallis H=6.37, 3 d.f., p=0.096 n.s. 1990; Kruskal-Wallis H=4.89, 5 d.f., p=0.43 n.s. 1991: Figures 8.5a & 8.5b). Bowing was a relatively uncommon behaviour where floor effects might have influenced the result (Martin & Bateson 1986), so whether individuals did or did not bow was tested using the χ^2 test in addition (see Methods). The result was not significant for either year (1990: χ^2=6.2, 3 d.f., p=0.10 n.s.; 1991: χ^2=4.8, 5 d.f., p=0.44 n.s.).

8.3.7 Alarm bowing

Alarm bowing was scored as the number of bows in a sample, not the amount of time spent alarm bowing as for the behaviour patterns analysed above (see Methods). Adults and younger immatures seemed to alarm bow less often than older immatures. There was a significant overall effect in both years. Post-hoc testing showed significant pairwise interactions between adults (which alarm bowed less often) and all other age classes in 1990, and between adults and the 1984-85

Figure 8.5a: Mean proportion of time (± 1SE) spent Bowing by birds of known age in 1990

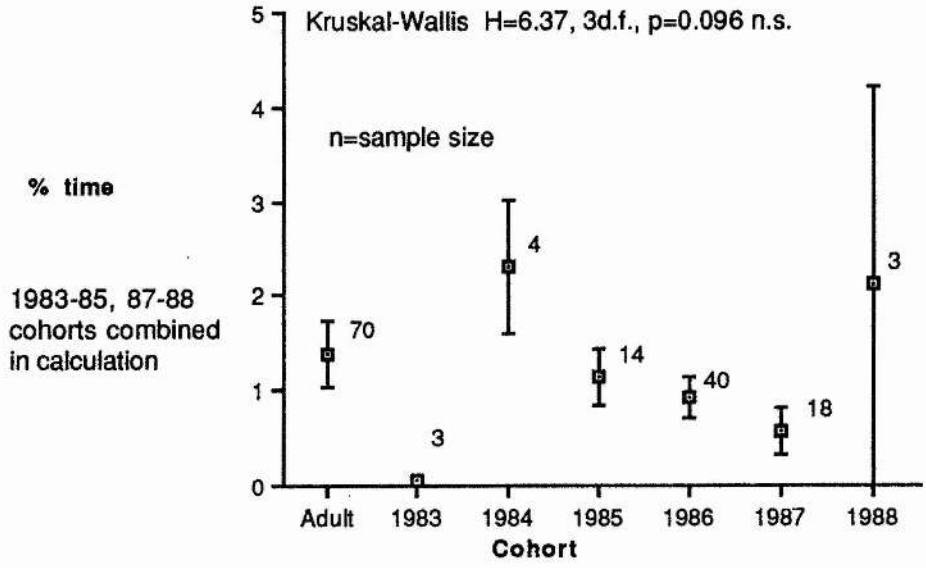
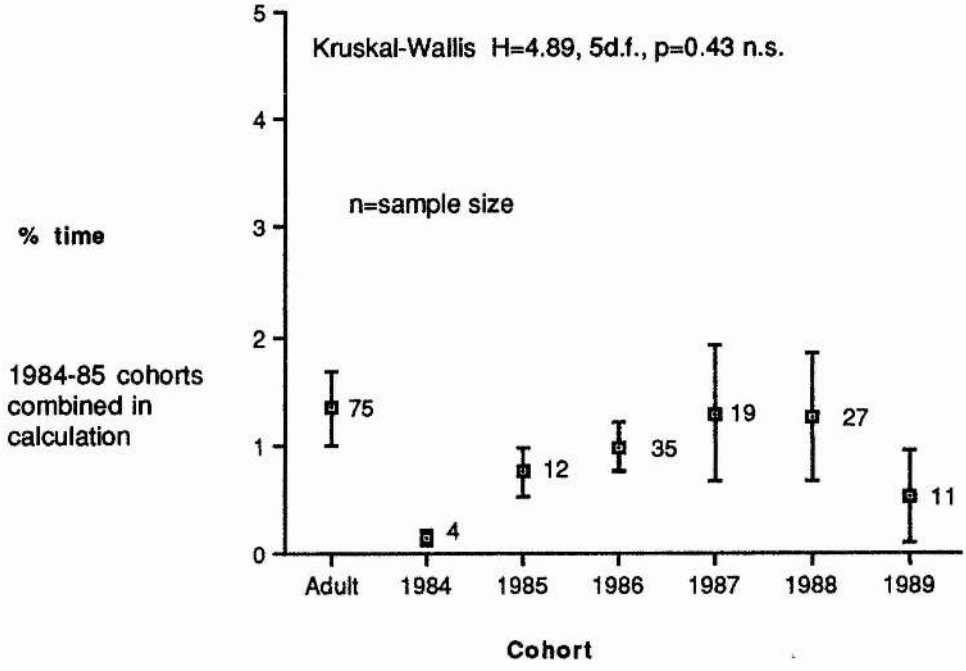


Figure 8.5b: Mean proportion of time (± .1SE) spent Bowing by birds of known age in 1991



and 1986 cohorts in 1991. The pairwise comparison between the 1986 and 1988 cohorts was also significant in 1991 if the adult age class was excluded from the calculations, the younger cohort alarm bowing less frequently (Figures 8.6a & 8.6b).

8.3.8 Mutual bowing

Mutual bowing was an uncommon behaviour pattern; analysis for differences in its frequency between cohorts was therefore carried out using χ^2 tests on whether or not an individual performed it. Where an individual was sampled more than once in a year the sample used was chosen at random (Methods). There was no significant difference between age classes in 1990 (Figure 8.7a). The test could not be performed on the data for 1991 as no meaningful combination of age classes led to <20% of cells having an expected frequency <5 (Siegel & Castellan 1990) (Figure 8.7b).

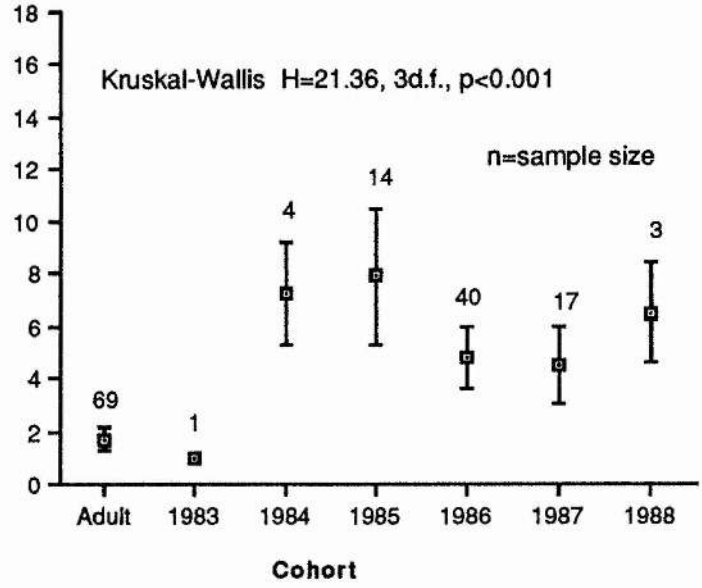
8.3.9 Ritual Walking

Ritual walking was similarly uncommon and analysed using χ^2 tests as for mutual bows (above). There were marked differences between age classes in the prevalence of ritual walking in both years (Figures 8.8a & 8.8b). Specifically, ritual walking was very uncommon in adults. This however, might have been an artefact of the single site and narrow ledge sites occupied by most ringed adults (see Methods).

8.3.10 Agonistic behaviour

The three agonistic measures—neck pointing, jabbing and fighting (Methods) were combined and their occurrence in each year compared between classes using χ^2

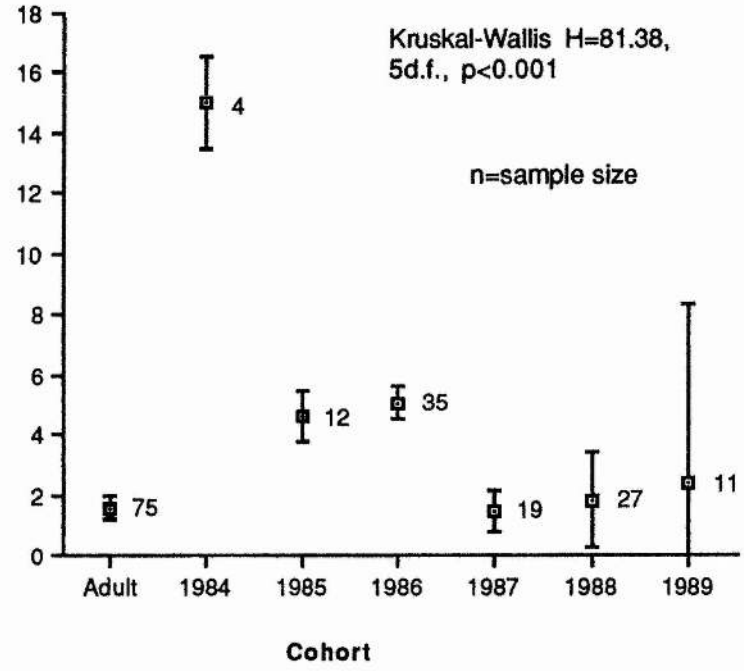
Figure 8.6a: Mean frequency of Alarm Bowing (± 1SE) by birds of known age in 1990



1983-85, 87-88 cohorts combined in calculation

Multiple-comparisons posthocs: Adults vs. all other cohorts significant, p<0.05. All other pairwise comparisons n.s.

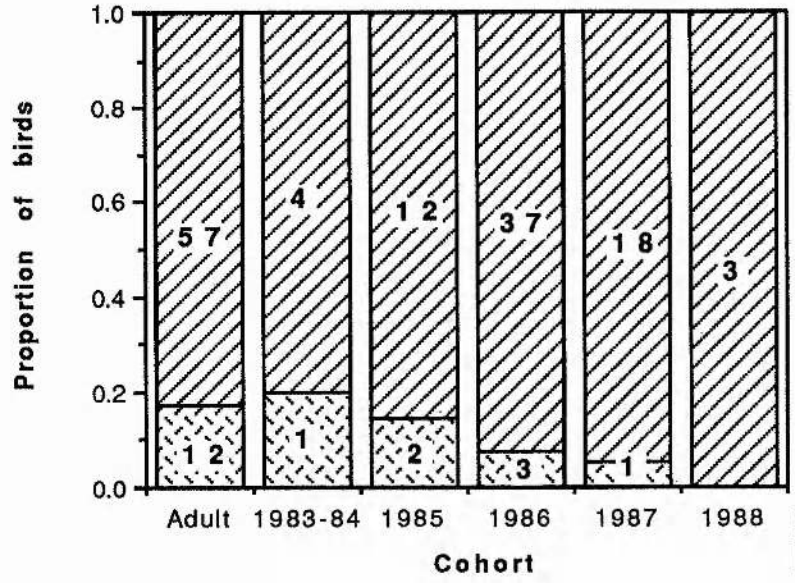
Figure 8.6b: Mean frequency of Alarm Bowing (± 1SE) by birds of known age in 1991



1984-85 cohorts combined in calculation

Multiple-comparisons posthocs: Adults vs. 1984-85, 1986 cohorts significant, p<0.05. All other pairwise comparisons n.s.

Figure 8.7a: Proportion of birds of known age Mutual Bowing in 1990



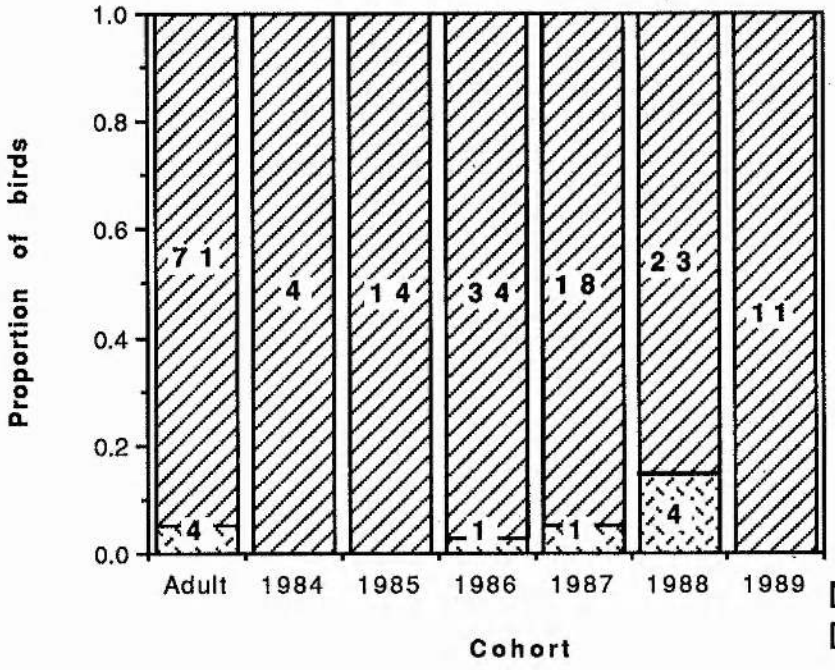
n=number of birds in category

Chisq.=3.72, 2d.f., p=0.16

1983-85, 1986-88 cohorts combined in calculation.

No Mutual Bowing
Mutual Bowing

Figure 8.7b: Proportion of birds of known age Mutual Bowing in 1991



n=number of birds in category

Chi squared not calculable. No meaningful combination of data resulted in <20% of cells having expected frequencies of >=5.

No Mutual Bowing
Mutual Bowing

Figure 8.8a: Proportion of birds of known age performing Ritual Walks in 1990

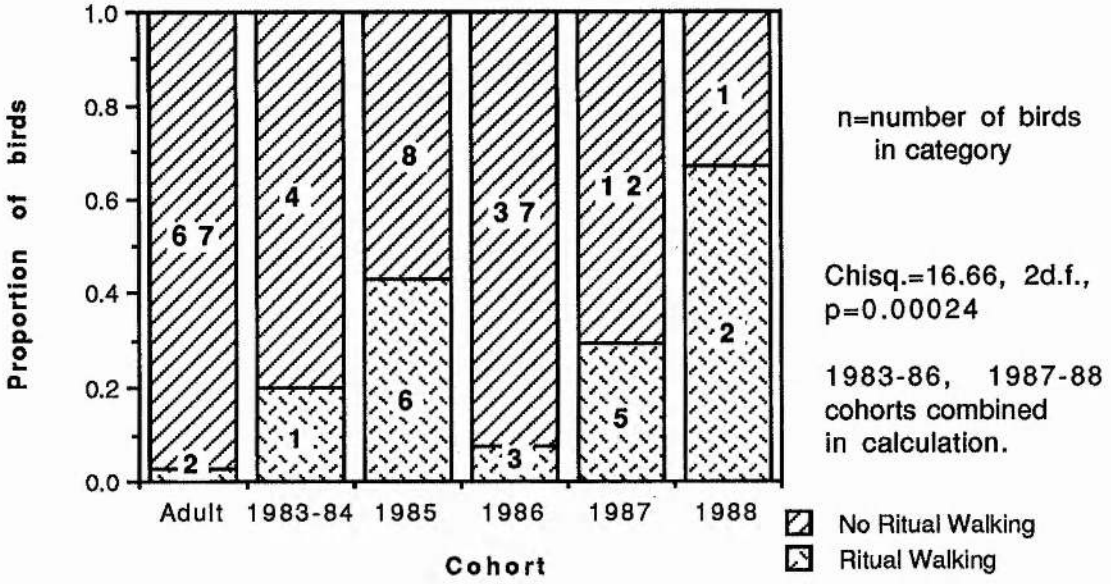
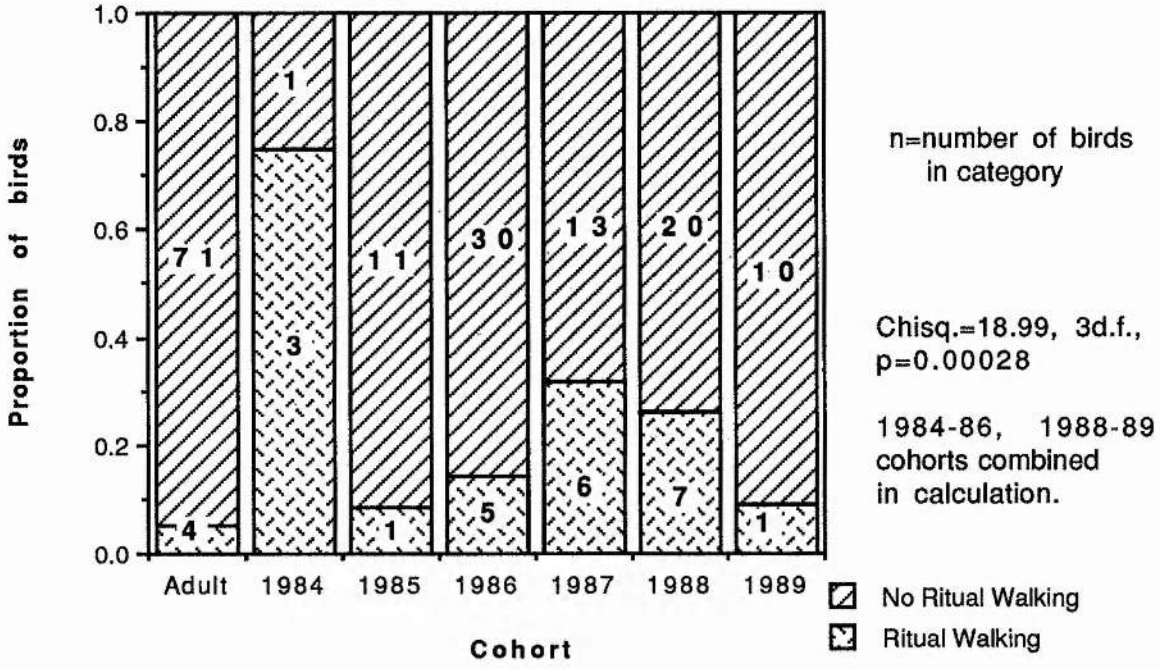


Figure 8.8b: Proportion of birds of known age performing Ritual Walks in 1991



tests (see section 8.3.7, Methods). In both years, younger birds were significantly more likely to engage or be engaged in agonistic encounters than older age classes (Figures 8.9a & 8.9b).

Older birds were significantly more likely to start fights than those from younger cohorts in 1990 (Figure 8.10a) but not in 1991 (Figure 8.10b). Older birds were also more likely to win fights in both years (Figures 8.11a & 8.11b). In 1991 the adult age class was excluded from the calculation since very few (4) agonistic encounters were recorded and the class could not be meaningfully combined with any immature cohort. For both these calculations, where more than one fight was recorded in a year for an individual, only one result (chosen at random) was used.

8.3.11 Other behaviour

Other behaviours measured (fish presentation, pebble carrying, and mating) were too rare within samples to permit statistical analysis. The mean % of time spent performing these behaviours was less than 2% in all age classes in both years, and the median and modal prevalence was 0 for all of them.

8.3.12 Between years comparisons

Data from individual cohorts were also compared between years to investigate whether behaviour changed significantly as birds aged. Wilcoxon matched pairs tests were used on individuals seen in both seasons. No birds from the 1983 cohort were seen in both years, and all (3) birds from the 1984 cohort seen in both years bred in 1991 and so were excluded. The 1989 cohort, birds from which first returned to the colony in 1991, could not be tested. The data from these tests are summarised in Table 8.2.

Figure 8.9a: Proportion of birds of known age class involved in Agonistic interactions in 1990

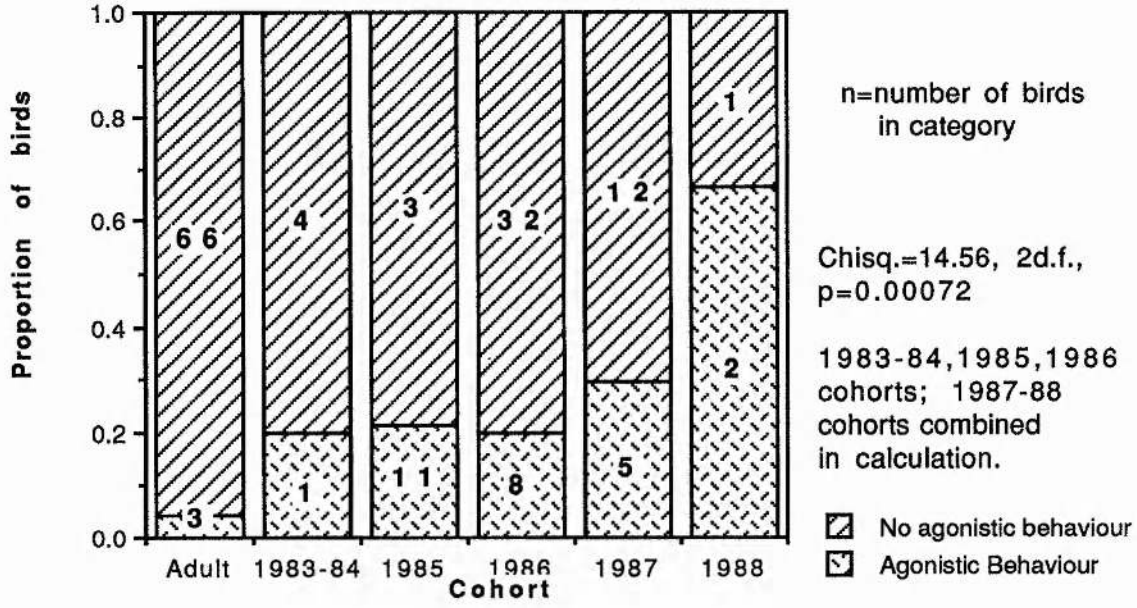


Figure 8.9b: Proportion of birds of known age involved in Agonistic interactions in 1991

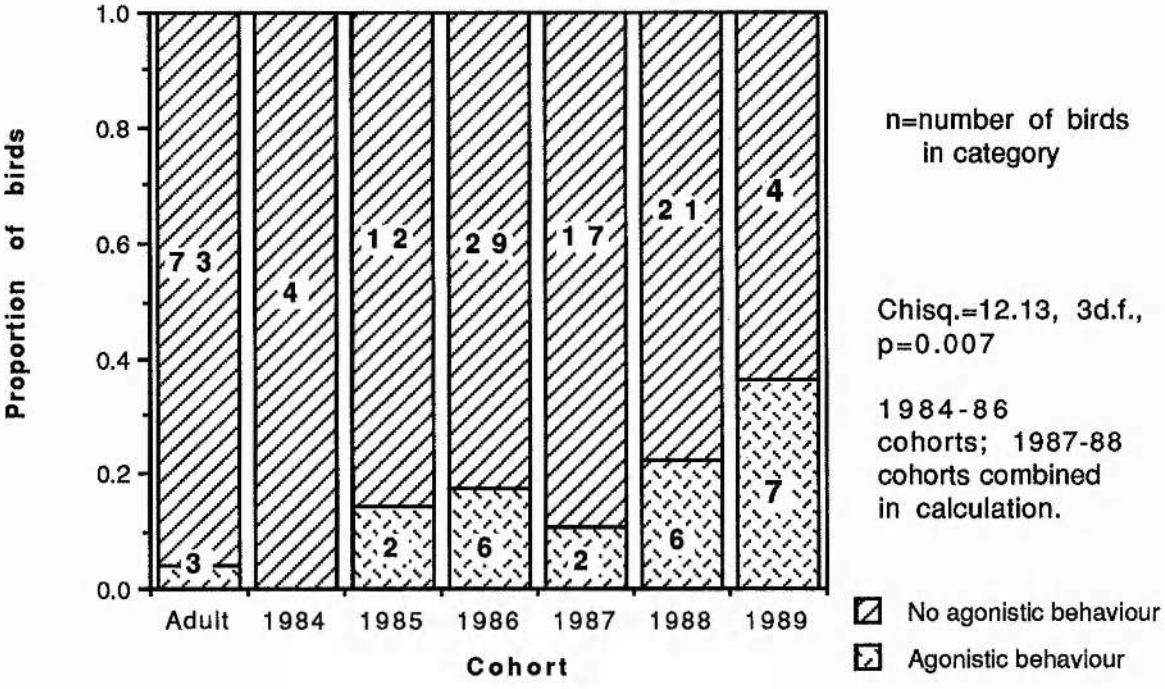


Figure 8.10a: Proportion of birds of known age initiating agonistic interactions in 1990

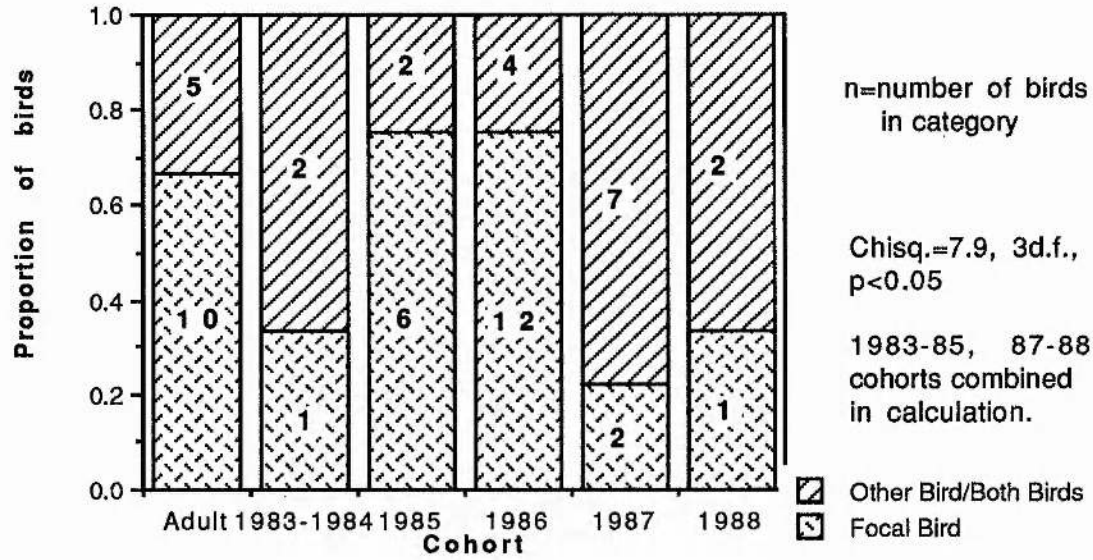


Figure 8.10b: Proportion of birds of known age initiating agonistic interactions in 1991

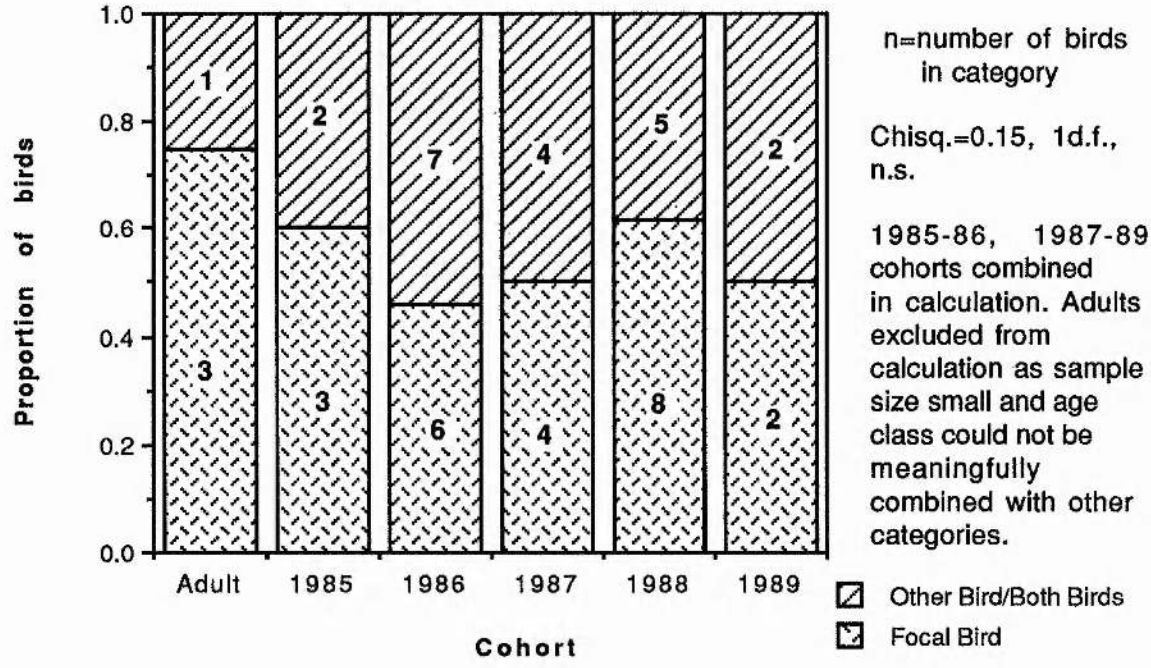
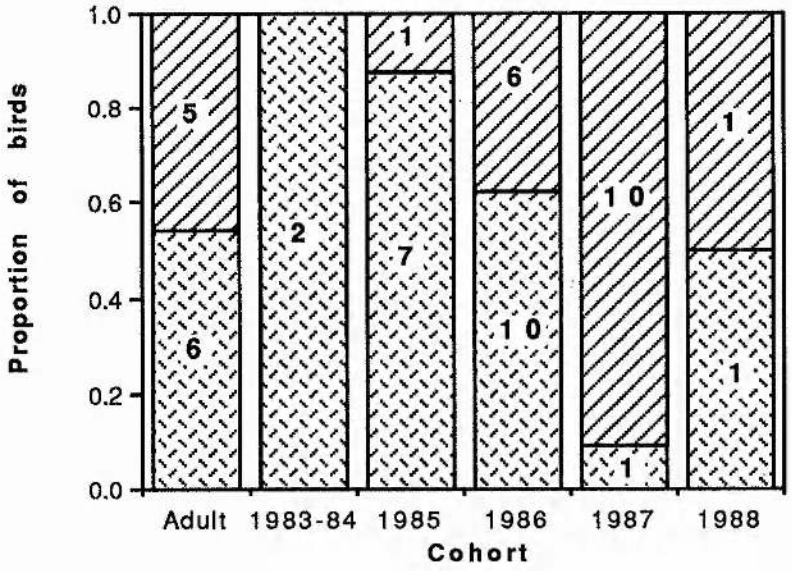


Figure 8.11a: Proportion of birds of known age which won agonistic encounters in 1990



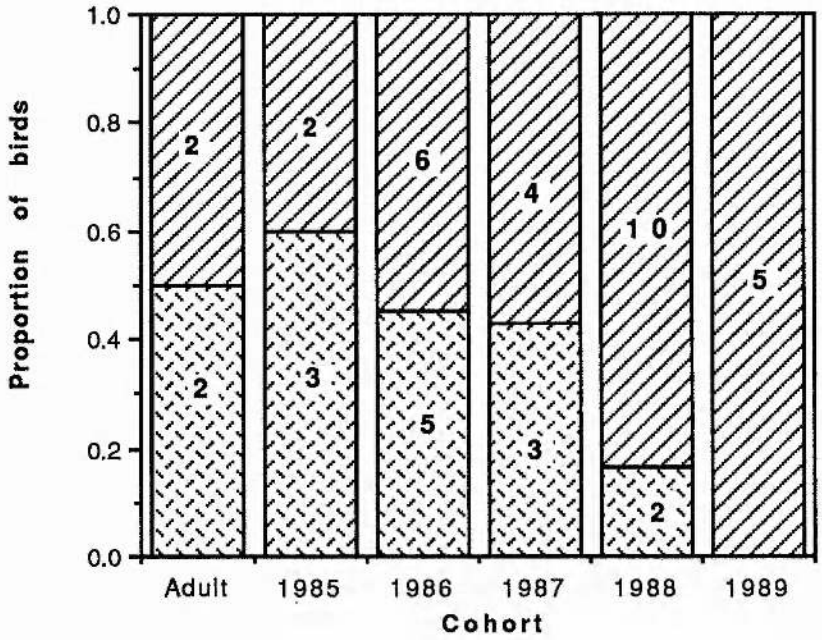
n=number of birds in category

Chisq.=13.48, 3d.f., p=0.0037

1983-85,1987-88 cohorts combined in calculation.

Lose/Draw
Win

Figure 8.11b: Proportion of birds of known age winning agonistic interactions in 1991



n=number of birds in category

Chisq.=5.11, 1d.f., p=0.024

1985-87, 1988-89 cohorts combined in calculation. Adults excluded from calculation as sample size was small and could not be meaningfully combined with other categories (see text)

Lose/Draw
Win

With few exceptions, cohorts did not vary significantly in behaviour between years; however, the sample size was generally small. Birds from the 1985 cohort ritual walked (a passive appeasement display: Birkhead 1978) less and alarm bowed less in 1991 than in 1990; the result suggesting that they spent less time engaged in mutual bowing (a site ownership display, probably with a pair-bonding element: Birkhead 1978) approached significance (Table 8.2). The 1986 cohort bowed (a site-ownership display: Birkhead 1978) more often in 1991 than 1990 and spent less time facing out. Adults also spent less time facing out in 1991 than in 1990 (Table 8.2); this result was unexpected, and the reasons underlying it are not clear.

Changes between years in whether birds were likely to start and to win agonistic interactions were assessed using χ^2 or Fisher Exact tests. Where birds were recorded in agonistic interactions more than once (in one or both years), the sample used was selected at random so that there was a single data point for each bird. Results are summarised in Table 8.3. Birds of the 1988 cohort were more likely to start the agonistic encounters they engaged in 1991 compared to 1990. All other comparisons were not significant.

8.3.13 Sex Differences

Data on the effect of sex differences on behaviour was difficult to obtain because guillemots, especially immatures, are difficult to sex (Chapter 2). Table 8.4 gives the number of birds in each age class for which the sex was known in each year and from which behavioural samples were taken. Sex differences were tested for using the data from these individuals.

No significant differences were found between the sexes in most behaviours. The sole exception among immatures was in the 1985 cohort, where female birds (F) had a closer average nearest-neighbour distance than males (M) in 1991 (F:

Table 8.2: Between years comparisons of guillemot behaviour

Behaviour	Age Class	N[a]	N for Test[b]	T	Sign[c]	Probability (Wilcoxon)
Face Out	Adult	34	16	74	-	0.78
	1985	9	9	28	-	0.55
	1986	20	16	110	-	0.03
	1987-88	9	9	24	-	0.90
Alert	Adult	34	34	448	-	0.01
	1985	9	9	13	+	0.29
	1986	20	20	104	+	0.98
	1987-88	9	9	27	-	0.64
Allopreen	Adult	34	31	280	-	0.53
	1985	9	9	13	+	0.29
	1986	20	14	19	+	0.04
	1987-88	9	6	2	+	0.09
Bow	Adult	34	28	245	-	0.34
	1985	9	9	32	+	0.29
	1986	20	17	59	+	0.42
	1987-88	9	4	7	-	0.58
Mutl Bow	Adult	34	12	52	-	0.31
	1985	9	5	15	-	0.06
	1986	20	7	13	+	0.93
	1987-88	9	0	-		-
Alarm Bow	Adult	34	24	206	-	0.11
	1985	9	9	45	-	0.01
	1986	20	19	78	+	0.51
	1987-88	9	9	24	-	0.86
Rit. Walk	Adult	34	16	58	+	0.62
	1985	9	8	36	-	0.01
	1986	20	12	47	-	0.53
	1987-88	9	7	15	-	0.93

[a] Number of individuals sampled in both years

[b] Number of individuals where level of behaviour not identical in both years. All ties were the result of the bird not performing the behaviour in either year

[c] Negative sign: behaviour performed more in 1990; positive sign: behaviour performed more in 1991

Table 8.3: Age-related changes within age classes in the proportion of birds initiating and winning agonistic interactions.

Age Class	Number of[b] interactions initiated by focal/other bird in 1990	Number of[b] interactions initiated by focal/other bird in 1991	Test	p
Adult	10/5	3/1	Fisher	n.s.
1985	6/2	3/2	Fisher	n.s.
1986	12/4	6/7	Fisher	n.s.
1987	2/7	5/4	Fisher	n.s.
1988	1/2	8/5	Fisher	<0.05
Age Class	**Number of interactions won by focal/other bird in 1990**	**Number of interactions won by focal/other bird in 1991**	**Test**	**p**
Adult	6/5	2/2	Fisher	n.s.
1985	7/1	3/2	Fisher	n.s.
1986	10/6	5/6	X^2[a]	n.s.
1987	1/10	3/4	Fisher	n.s.
1988	1/1	2/10	Fisher	n.s.

[a] $X^2=0.77$, 1 d.f., $p>0.05$ n.s.

[b] Where an individual was recorded in an agonistic interaction more than once in one or both years, only one sample, selected at random, was used in the test (see text).

Table 8.4: Numbers of birds of known sex from which behavioural samples were taken in each field season

Age Class	Male 1990	Female 1990	Male 1991	Female 1991
Adult	32	24	30	42
1983	0	0	0	0
1984	1	0	0	0
1985	4	4	3	4
1986	4	5	5	4
1987	4	0	2	2
1988	0	0	4	1
1989	-	-	1	0

0.95±0.04 bird lengths; M:1.28±0.08 bird lengths. Mann-Whitney W=10, n_1=4, n_2=3, p=0.04). The apparent tendency for males of the 1986 cohort to spend more time facing out than females in 1990 approached significance (F:45.5±7.9%; M:75.9±6.45%. Mann-Whitney W=18, n_1=5, n_2=5, p=0.06 n.s.). Adult males showed a significant tendency to be further from their nearest neighbour than adult females in 1990 (F:0.74±0.14 bird lengths; M:1.32±0.19 bird lengths. Mann-Whitney W=615, n_1=25, n_2=34, p=0.039), and to alarm bow less often than females in 1991 (F:1.97±0.54 bows/sample; M:1.33±0.88 bows/sample. Mann-Whitney W=1762, n_1=43, n_2=30, p=0.03).

There were no sex differences in any age class in the propensity of a bird to start agonistic encounters or to win them (Fisher Exact Tests, n.s.).

8.4 Discussion

The presence or absence of individual birds, especially immatures, could not be predicted and subject selection depended wholly on which birds were present. As a result, there was considerable variation in the number of samples taken for each bird. Results for each individual were therefore averaged to give the score used in the test, or, where this was not appropriate, data from one sample was selected at random (Methods). As a result, the effective sample size was considerably reduced. The exclusion of adult birds incubating or brooding chicks, and postbreeding females, was also necessary as they clearly differed in a separate dimension than age from immatures. The shortcoming of this approach is that the range of adults available was larger in the earlier part of the season since pair members not incubating/brooding did not remain on site for long periods. Many of the adults available later were birds which had not bred or whose attempt had failed. These may have been poorer quality individuals unrepresentative of the adult population as

a whole. A further problem, with between years comparisons, was that there was no way of controlling for year effects which may have influenced behaviour.

This method of measuring behaviour was also restricted to birds settled on sites. Ten hour-long watches at the Dense subcolony in June 1991 suggested that birds which were apparently immatures did attempt to land there, but were almost always unable to settle, as they were ejected by adults. As very few of these birds were ringed, and they often appeared to attempt to land several times in succession, the age and number of these birds was uncertain, although some at least (4 individuals) were immatures which attended the top ledges above Dense. This suggests that top ledge attending birds did try to move onto sites within Ledge and Broad ledge subcolonies, but were normally unable to do so. Immatures arriving at a single-site subcolony (South Face) where matching observations were made landed successfully on unoccupied sites or half sites, but were ejected if they attempted to land at a site occupied by an adult.

The general pattern of observed behaviour of settled birds was for adult birds to differ markedly from immatures, but for immatures to vary little between cohorts or between years. More specifically, adults tended to be found closer to other birds, to engage in allopreening more often, to spend less time alert and facing out, to perform fewer alarm bows, and to engage in agonistic interactions less often. They did not, however, spend significantly more time in site-maintenance behaviours such as bowing or mutual bowing than immatures, as might have been expected. The pattern of face-out and alert behaviour suggests that adults were less concerned with external events than immatures. Immatures spent much of their time alert and in face-out positions where other birds could be observed, typically peering down at the adult ledges from top sites for long periods.

There were few sex differences in behaviour, which might be expected in a sexually monomorphic species. Adult females had a smaller nearest neighbour distance than adult males in 1990, and 1985 cohort females had a smaller nearest neighbour distance than 1985 cohort males in 1991, when the cohort was six years old. Adult females alarm bowed more often than males in 1990. The reason for the difference in nearest-neighbour distance in adults may be that in the prelaying period males are alone at the site three times as often as females; later, birds are alone at the site more or less equally often (Wanless & Harris 1986). This would result in an apparent lower nearest-neighbour distance for females. The 1985 data may indicate that females of that age were more likely to be paired than males; the small amount of evidence available on sex differences in recruitment (Chapter 7) suggests that females may recruit at a younger average age than males. Why adult females should alarm bow more often than adult males is unclear.

In several species of seabird, e.g. wandering albatross (Pickering 1988), gannet (Nelson 1978), sooty tern (Harrington 1974), and in some respects kittiwake (Monnet *et al* 1992), a process which may be termed 'behavioural maturation' has been noted for immature birds as they get older—the level of site acquisition/maintenance displays and of pairing/sexual activity increases, the birds are more tenacious in, and successful at, agonistic encounters, and perform appeasement displays less often. This trend has been interpreted as the result of greater experience, motivation and/or physiological maturity as individuals age (Pickering 1988). Another potential influence noted for breeding birds, which may apply to immatures, is differential survival of individuals based on intrinsic quality, so that the surviving population is of higher average quality as birds age (Coulson & Wooller 1976; Bradley *et al* 1989; Aebischer & Coulson 1990; Wooller *et al* 1990).

The data lend some support for the occurrence of a degree of behavioural maturation in guillemots for pairing/sexual behaviours and, to a lesser extent, site acquisition/maintenance. Although immatures in general differed little between cohorts, or within cohorts between years, and where there was a significant difference between immature cohorts in one year the result was seldom replicated in the other year, where significant differences were found they were in the direction predicted by the behavioural maturation hypothesis. Birds of the 1984-85 cohorts had a closer average nearest neighbour distance than the 1988 cohort in 1991, and birds of the 1985 cohort alarm bowed and ritual walked (a passive appeasement display) less often in 1991 than in 1990. Birds of the 1986 cohort were involved in allopreening bouts more often in 1991 than 1990 (suggesting that they were paired more often) and spent less time facing out (possibly indicating greater average levels of attachment to a site, as for adults). The graphed trend for several behaviours (e.g. nearest-neighbour distance in 1991, proportion of time spent facing out and alert), although pairwise interactions were not significant, was also consistent with a shift with age to more "mature" behaviour and there were no clear cases between cohorts of a trend in the opposite direction to predictions. However, the tendency of birds of the 1985 cohort to take part in mutual bowing (primarily a site-ownership display) dyads less often in 1991 than in 1990 approached significance, contrary to expectations if behavioural maturation were occurring.

The pattern of agonistic behaviour is also consistent with behavioural maturation, in that older immature cohorts were more likely to start agonistic interactions in 1990 and to win them in both years; younger cohorts were more likely to be involved in agonistic encounters, but tended to lose.

Four main reasons, not mutually exclusive, have been advanced to explain deferred maturity in seabirds: 1) physiological immaturity (Ainley 1978, Hector *et al* 1986); 2) the need to perfect foraging skills and local knowledge of foraging areas (Burger

1990 for a review); 3) the need to find a partner and establish a pair bond (Pickering 1989; Nelson 1989); 4) securing a good quality breeding site (Potts *et al* 1980; Porter & Coulson 1987; Porter 1990). Of these, the evidence in this chapter, on the activity of birds while at the colony, can address hypotheses 3) and 4).

There does seem to be some evidence consistent with the development of pair-bonding skills. Where significant effects are found in behaviours which may be related to pairing, e.g. allopreening and proximity to other birds, they are in the direction which would be predicted. Hudson (1979), however, found that (younger) immatures on sea rocks mated more often than (older) immatures on the colony; but the incidence of temporary pairings in his population increased with age, as the evidence here also suggests. The overall effect is weak, however. In some species of seabird, immatures may pair permanently one or more seasons prior to recruitment (e.g Procellariiformes in general (Croxall 1991), gannet (Nelson 1978)). There is no evidence that guillemot pairings in years prior to recruitment are more than temporary; these may function to practice behaviour and/or involve reciprocal altruism, as the major activity of temporarily paired birds is allopreening. Guillemots lack the elaborate and often extended sexual advertisement/ pairing displays found in many other seabirds (e.g wandering albatross (Pickering 1988); gannet (Nelson 1978); shag (Aebischer 1985)), further implying that factors other than establishing a pair-bond are more important in the recruitment dynamics of the species.

Choice of nest site can have important consequences for reproductive success in guillemots (Birkhead 1977; Chapter 7). Perhaps surprisingly, evidence of increasing levels of site-ownership activities as immatures age is weak, and in one case a trend approaching significance runs contrary to expectations. However, in contrast to pairing behaviour, which presumably involves cognitively complex considerations such as assessment of potential mate quality, as well as learning to

co-ordinate behaviour, site-ownership displays are relatively simple and stereotyped. A consequence of variations in quality of breeding site, which in guillemots may be related to nest site density (Birkhead 1977, Chapter 7), is competition for sites. On the Isle of May, immatures were almost always found on top ledges or peripheral sites, and not among breeding birds (Chapter 6); immatures attempting to land at broad ledge subcolonies or at adult sites in single-site subcolonies were almost always ejected immediately. Sites on top ledges or peripheral to the breeding group would not be of high quality and so, if held by immatures, would not demand high levels of site ownership display. Acquiring a site in the established breeding area would require high levels of ability in agonistic encounters, and older birds were more likely to start and to win agonistic encounters than younger cohorts. Only after a site had been won would site ownership displays be necessary, and on the Isle of May all known-age birds occupying sites in established breeding areas bred or attempted to breed.

Despite some evidence consistent with behavioural maturation, on most measures the oldest cohorts still differ quite considerably from adults, and are more similar to other immature cohorts. This trend differs with that from the extensive studies of the development of foraging in seabirds, which have shown a general and progressive increase in proficiency in a wide variety of species, usually reaching adult levels in the year of recruitment or the previous year (Orians 1969; Dunn 1972; Verbeek 1977; Morrison *et al* 1978; Searcy 1978; Greig *et al* 1982; Porter & Sealey 1982; Carrol & Cramer 1985; Maclean 1986. Burger 1990 for review). The lack of a similar, more smoothly sloped transition in guillemot activity at the colony may be due to a sudden phase shift in ability and/or motivation, but is more likely to be due to other factors. A greater proportion of immatures attend the colony, and the amount of time spent there increases, as they age, and an apparent effect of experience enhancing levels of colony attendance (Chapter 5) may in fact reflect differences in individual quality. If this is so, behavioural samples, particularly in

younger cohorts, may be of higher quality individuals on average, depressing the apparent differences between cohorts in behaviour. Also, a substantial proportion of the 5 and 6 year old cohorts were known, or inferred, to have recruited (Chapter 7). The remaining nonbreeders from these cohorts, from which behavioural measures were taken, may have been relatively unfit and behaviourally less mature individuals, which would also depress the apparent difference in behaviour between immature cohorts. In addition, the average age of adult birds will have been considerably older than 7 years, so that the difference in the average level of experience and motivation (Trivers 1972; Clutton-Brock 1991) would be higher than the single year increment separating the immature age classes. Also, there is an obvious shift in circumstances between adults and immatures. Adults were almost always paired and had sites, whereas immatures generally had neither. This factor by itself can account for the large observed differences between adults and immatures in behaviour, and large intrinsic differences in physiology, motivation and experience need not be inferred from the present data (though they may occur).

In summary, the evidence from activity at the colony suggests that there are considerable differences between adults and immatures in behaviour, but that differences between immature cohorts are in general relatively small. Adults appear to be less concerned with events external to themselves and their sites than immatures. There is some evidence consistent with levels of behaviour "maturing" in the direction of greater levels of pairbonding behaviours, ability to compete in agonistic encounters, and (weakly) greater levels of site ownership behaviour as immatures age, but the role of potential causal factors underlying these trends—age, experience, motivation and differential survival—remain speculative and would repay more detailed investigation. The data presented here suggest that the ability to compete for a site may be of particular importance in the dynamics of recruitment.

Chapter 9

Concluding comments

In this chapter I briefly consider the general pattern of behaviour of immature guillemots in relation to that of other seabirds, and in relation to broader aspects of guillemot adaptation and population dynamics. Detailed discussions of particular aspects of behaviour and ecology have been included in the relevant chapters. Some unresolved problems in guillemot recruitment ecology will be outlined, and future directions of research suggested.

To summarise the main findings of this study, the mortality rate of immature guillemots appears to be highly variable in the first year of life, and is probably related to the environmental conditions in the immediate post-fledging period. However, there is no evidence that this directly affects the size of the breeding population. Survival usually balanced the mortality rate of adults, and was often considerably in excess of adult mortality. Figures on recruitment in 1991 were difficult to reconcile with observed population trends, the discrepancy probably reflecting errors in estimates of survival, populations, and recruitment levels. Considerable movements of immatures between colonies occurred, but the extent to which birds recruited into non-natal colonies was unknown although some such recruitment did occur.

Birds did not return to the colony before age 2; thereafter the proportion of the cohort attending the colony rose, and birds both arrived earlier in the season and spent more time at the colony up to the age of 4-5 years, after which levels were broadly stable. Most 2-3 year olds began attending at club sites below the colony but, both in the course of the season and between seasons, birds tended to move to

areas in or above the breeding colony. At these sites, birds were highly sedentary and became increasingly so with age. Most birds were only ever seen at one subcolony, and usually chose the subcolony at which they had hatched. The activity of immatures at the colony varied little as they grew older, although it differed considerably from the behaviour of (non-brooding) adults. There did appear to be some tendency for older birds to be paired more often, although such pairings appeared to be temporary, to show lower levels of alarm and appeasement, and to be involved in fewer agonistic encounters. However, compared with younger immatures, they were more likely to start and to win the fights in which they were involved. During the main study period, recruitment did not begin until 5 years old and most birds appeared to recruit at 6. Levels of recruitment were difficult to quantify, but there was a suggestion that younger birds may recruit onto fringe sites more often then older recruits, and that female recruits were younger on average. The breeding success of recruits was substantially lower than that of established breeders.

The data on survival levels of immatures, in relation to adult mortality and population trends, suggests that there is no simple connection between survival rate and changes in the breeding population, and that at present immatures are likely to be in competition for opportunities to recruit. How this affects immature behaviour is unclear. Future information on behaviour and on recruitment levels in the two cohorts where survival appeared to be especially high, 1986 and 1988, may help to clarify this subject.

The general pattern of immature behaviour in guillemots seems to be similar to that of other species studied. In immature guillemots, a greater proportion of the cohort attended the colony with age. Birds arrived at the colony earlier in the season as they grew older and/or more experienced, and spent more time there. Similar patterns of attendance have been observed in Manx shearwater (Perrins *et al* 1973),

razorbill (Lloyd & Perrins 1978), gannet (Nelson 1978a), Adelie penguin (Ainley *et al* 1983), puffin (Harris 1983), pigeon guillemot (Nelson 1987), kittiwake (Porter 1988), and Brünnich's guillemot (Noble 1990; Gaston 1991). Younger birds attended clubs of immature birds, similar to skuas (Davis 1976; Klomp 1991) and gannets (Nelson 1978a), although guillemots moved to sites in or above breeding areas as they grew older. Philopatry to the natal area of the colony was strong, as in other species for which data are available - Manx shearwater (Harris 1966; Perrins *et al* 1973); herring gull (Chabrzyk & Coulson 1976); puffin (Harris 1983); and shag (Aebischer 1985). Immatures commonly visited, and sometimes recruited into, colonies other than the natal colony, as in storm petrel (Scott 1970), herring gull (Chabrzyk & Coulson 1976), Manx shearwater (Brook 1978), gannet (Nelson 1978a), puffin (Harris 1983), and shag (Aebischer 1985).

Two important aspects of immature guillemot behaviour and ecology which appear to differ from the general pattern in seabirds are the large variations in postfledging survival from year to year and the relative lack of development in sexual/pairing activity as birds become older. These appear to be consequences of the most specialised aspects of guillemot breeding biology, semi-precocial fledging and high density nesting.

While pre-fledging mortality in seabirds can be very variable, there are few reports of year-to-year variation in postfledging survival as extreme as in guillemots. Studies of puffin (Harris 1983), kittiwake (Porter & Coulson 1987), and roseate tern (Nichols *et al* 1990) showed no marked variations between years, but there was strong variation between years in the closely related (and semi-precocial) Brünnich's guillemot (Noble *et al* 1991). The strong correlation between subsequent return rates in guillemots and the weather conditions in the first three months a cohort is at sea suggests that the variation in survival rate is a non-adaptive consequence of a selected trait, semi-precocial fledging. It would appear

that the guillemot's offshore feeding niche and inability to transport more than one food item at a time has resulted in energetic constraints which have produced a breeding system where the chick goes to sea while only partially developed, where it is closer to its food supply. The cost of this behaviour appears to be that chicks at sea are highly vulnerable to adverse weather conditions through direct exposure and/or separation from the parent bird.

At a behavioural level, the large variations in the survival rates of different immature cohorts may have profound effects on the recruitment process. The level of competition for sites and/or high quality mates will vary considerably depending on the size of the surviving cohort to which an individual belongs, and that of other, particularly older, cohorts. In conjunction with variables such as food supply and nest site availability this may have profound effects on the opportunities for, and constraints on, recruitment for individual birds.

Guillemots nest at densities higher than any other bird (Birkhead 1978), yet are highly territorial. A number of displays advertise site-ownership, and there are several ritualised agonistic displays, but no there are no unambiguous sexual advertisement displays - prominent features of the behaviour of many other seabirds (e.g. Pelecaniformes (Van Tets 1965), albatrosses (Meseth 1965; Pickering 1988), penguins (Stonehouse 1975), and terns (Fisher & Lockley 1954)). This suggests that maintaining a breeding site is particularly important for adult guillemots, and that obtaining a site is the major prerequisite for recruitment in immatures. Established breeders are usually faithful to their sites and defend them vigorously, and so in order to acquire an established site with an experienced mate (which have higher levels of breeding success in most species - Wooller *et al* 1992 for review) an immature would be at an advantage if it had a detailed knowledge of part of a colony. This would allow the bird to take advantage of deaths or disappearances of established birds very quickly, probably acquiring an experienced mate in the

process. This may explain why immatures typically attend the same small area of the colony throughout their pre-recruitment period (after moving from clubs) and show little sign of more than temporary pairings.

If acquisition of a mate is secondary to the acquisition of a site, mate choice for most guillemots may simply be a function of which bird of the opposite sex jointly occupies the breeding site (which may itself be a measure of the bird's quality); this would account for the lack of sexual advertisement displays.

The pattern of behaviour in immature seabirds outlined above appears to be adaptive, as much the same pattern is found in four different orders (Charadriiformes, Sphenisciformes, Pelecaniformes and Procellariiformes) which do not appear to be closely related evolutionarily (Wetmore 1960). Variations in behaviour between species, which in guillemots appear to result from particular details of their breeding ecology, suggest that a comparative approach may be useful in understanding the evolutionary factors shaping the behaviour of immature seabirds.

Although few immatures were of known sex, there were indications that factors such as recruitment age and age of first return to the colony may be related to gender in guillemots, as in other species (e.g. shag, Potts *et al* 1980; wandering albatross, Pickering 1988; kittiwake, Porter & Coulson 1987). This is an important area of recruitment biology, and there should be scope to reassess the current data when the sex of more of the birds followed in this study is determined as they recruit into the breeding population.

At its simplest, four proximate factors regulate breeding populations : 1) Adult mortality; 2) productivity rates 3) survival of immatures to recruitment and 4) rates of immigration and emigration. For the Isle of May guillemot population,

assessment is rather more complex than this might suggest as, although adult mortality and productivity were broadly stable, immature survival was highly variable between cohorts, apparently because of density independent factors. Recruitment age was also variable, probably differed between cohorts, and may have been related to the size of a cohort and of other, particularly older, cohorts (assuming that there was competition for opportunities to breed). Conditions early in life possibly reduced the fitness of some cohorts (e.g. of birds hatched in 1984). The considerable movements of immatures between colonies suggest that immigration and emigration may be much more common in guillemots than previously thought. A priority in future work in this and other species must be to determine whether the widescale movement of immatures between colonies is followed through into substantial levels of intercolony recruitment. If this is the case, it will be important to quantify the levels of immigration and emigration, the sex ratio of immigrants and emigrants, and the social and ecological conditions affecting immigration and emigration. This is a challenging prospect, but without it an accurate view of population dynamics will not otherwise be obtainable if intercolony recruitment does occur frequently.

Further, the precision of some of the data is also open to question. Adult mortality was by itself sufficient to explain the whole of the population decline between 1990 and 1991, but immatures were recruiting into the breeding population at that time. The only escape from this implicit contradiction would be to assume a considerable increase in the number of adults not breeding, but there was no evidence that this occurred (Harris *pers. com.*). Also, known rates of immature survival (almost certainly underestimates) were close to or well in excess of adult mortality in all but one year despite a stable or declining population in the period when the older marked cohorts were recruiting. While it would be possible to construct population models on the basis of the data here, given the implied imprecision of some of the measures and the lack of data on others such a model would neither be likely to

mirror the actual mechanism of population regulation nor to be of use in estimating the influence of the unknown factors. More basic data, particularly on recruitment rates and their relation to cohort survival rates, and on immigration and emigration, is necessary before useful population models can be constructed.

The observed population changes over the last 20 years appear to be related to the food supply: there is evidence that guillemots compete for food in the breeding season (Birkhead & Furness 1985), and that the Isle of May population had more difficulty in provisioning chicks in the later 1980s than previously (Harris 1990). The proximate causes of these changes in population levels may be examined in relation to the present data. Although the data do not permit firm conclusions to be advanced, they do suggest which factors may be of particular importance. Unfortunately, little data is available for the period where guillemot populations on the Isle of May and elsewhere were expanding most rapidly in the late 1970s and very early 1980s. (Harris & Galbraith 1983; Harris 1990). However, from later work it appears that adult mortality varied little in guillemots on the Isle of May, and that productivity varies only over a fairly narrow range (Harris 1990). As the increase and subsequent decline of guillemots on the Isle of May was broadly in line with the E. North Sea population as a whole, differential immigration and emigration between colonies seems unlikely to have caused the increase and subsequent decline there. The remaining proximate factors are the survival rates of immatures and levels of recruitment, both of which are variable. Since neither of these are known for the period of increase, it is difficult to assess their influence on population growth. The apparent relationship of cohort survival rates to immediate post-fledging weather conditions suggests that the size of a cohort is primarily determined by an unpredictable and density-independent process. This may affect population growth rates, especially if competition for food and/or breeding sites is relaxed. In addition, conditions at this stage in life may have long-lasting effects on the fitness of surviving birds, affecting recruitment age. On balance, therefore, the

evidence suggests that variations in survival and recruitment rates are most likely to have been the immediate factors underlying population changes on the Isle of May

More generally, the body of evidence on survival and behaviour of immature guillemots and other seabirds has reached a stage where a general pattern of behaviour common to the group has been established. Many of the underlying factors which appear to cause and to influence the process of recruitment have been identified in the course of this work. Evaluation of the relative importance of these factors, and how they interact, is the next, if complex, stage in the process of understanding recruitment, and its wider role in seabird population dynamics and life history strategies.

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Appendix 1

EPSON HX-20 BASIC program for collecting behavioural data

```
10 REM Program to sample guillemot behaviour, continuous sampling method, by JA Graves; modified by DJ Halley

20 Option base 1

30 Clear 650,650

40 Data 81, SP, 87, SA, 69, TA, 65, RW, LD, 82, NK, 70, JB, 86, FT, 72, BW, 74, MB, 75, PB, 76, FP

50 Data 73, MT, 79, SL, 80, AP, 49, AL, 50, FA, 51, NF, 52, AB, 53, ER, 54, MV, 32, UD

60 Dim KY(22), M$(22), D1(300), E1(30), E2$(30)

70 NK=22

80 NS=300

90 NX=NS/10

100 For I=1toNK
```

```
110 Read KY(I), M$(I)

120 Next

130 For I=1toNK

140 E2$(I)="                "

150 Next

160 Input "Who   ";b$

165 Input "Sex";Q$

167 Input "Cohort";Z$

170 Input "Where";L$

175 Input "Nearest bird";T$

180 X$=Date

190 S$=Time

200 A$=S$

210 Gosub 890

220 S=E
```

```
230 C=0

250 A$=Inkey$

260 If A$=""goto 250

270 A=Asc(A$)

280 If A=13 goto 420

290 K=0

300 For I=1toNK

310 If A=KY(I) then K=I

320 Next

330 If K=0 goto 250

350 C=C=1

360 Print M$(K)

370 D1(C)=K

380 A$=Time$

390 Gosub 890
```

```
400 D2(C)=E-S

410 If C<=NS goto 250

430 K=0

440 For I=1toC

450 If d1(I)<6 or D1(I)>8 or k>NX goto 530

460 Print "Agonistic  ";M$(D1(I))

470 K=K+1

480 E1(K)=I

490 Input "With whom   ";A$

500 Input "Who started?";M$

510 Input "Who won";N$

520 E2$(K)=M$+N$+A$

530 Next

550 For I=1toC

560 If D1(I)<13 or D1(I)>15 or K>NX goto 610
```

```
570 Print "Sex          ";M$(D1(I))

580 K=K+1

590 E1(K)=I

600 Input "With whom";E2$(K)

610 Next

630 For I=1toC

640 If D1(I)<>21 or K>NX goto 690

650 Print "Move    ";M$(D1(I))

660 K=K+1

670 E1(K)=I

680 Input "To where";E2$(K)

690 Next

710 Open"O",£1, "CAS0:Obs"

720 Print £1,X$

730 Print £1, S$
```

```
740 Print £1, B$

745 Print £1, Q$

747 Print £1, Z$

750 Print £1, L$

755 Print  £1, T$

760 Print £1, using "£££";C

770 For I=1toC

780 Print £1, using "££";D1(I)

790 Print £1, using "££££";D2(I)

800 Next

810 Print £1, using "££";K

820 For I=1toNK

830 Print £1, using "£££";E1(I)

840 Print £1, E2$(I)

850 Next
```

```
860 Close

870 Print tapcnt

880 End

890 E=VAL(Left$(A$,2)*3600+VAL(Mid$(A$,4,2))*60+VAL(Right$(A$,2))

900 Return
```

Appendix 2

BASIC program for conversion of EPSON HX20-stored behavioural data into SQLLOAD compatible format

```
10 REM BASIC program to read guillemot behavioural observations and format to
ORACLE SQLLOAD. Programmed by SA Courtney, testing & modification by DJ
Halley

20 !>>> SAC MOD

                !*** initalize variables for later use

yes% =  0%

no%  = -1%

date% = no%

next_date$ = ""

new_sample% = 1%

keycode17_18% = 2%

keycode_rekey% = 3%

keycode_unknown% = 99%

flag% = 0%

error_flag% = no%

end_of_file% = no%

key17_18_max% = 200%

dim key17_18%( key17_18_max% ,1% )

count% = 0%

last% = 0%

last_state% = 0%

last_key_time = -9
```

```
!<<< SAC MOD
50 INPUT 'NAME FOR INPUT FILE' , INF$
55 OPEN  INF$  FOR INPUT AS FILE #1%
60 INPUT 'NAME FOR OUTPUT FILE' , OUTF$
65 OPEN  OUTF$ FOR OUTPUT AS FILE #5%
!>>> SAC MOD
!       allows large lines to be written to a file
70 NOMARGIN #5
!<<< SAC MOD
!       arrays for behavioural data :activity, duration, time key pressed,
!       whether activity reactive(with another bird)
100 DIM LKEY(100), DUR(100), LTIME(100), RA(100) 110 DIM
WHO_WITH$(50), WHO_START$(50), WHO_WON$(50) !>>> SAC MOD
!       used with the who_xxx arrays to determinte who the splitdata belongs to
dim who_splits%( 50, 1 )
dim ra_splits( 100 )
for n% = 1% to 50%
        who_splits%( n%, 0 ) = 0
        who_splits%( n%, 1 ) = 0
        ra_splits( n% ) = 0
        ra_splits( n% + 50% ) = 0
next n%
!<<< SAC MOD
120 DIM REKEY(40)
130 NRK% = 7
135 REKEY(1%) = 6
140 REKEY(2%) = 7
145 REKEY(3%) = 8
150 REKEY(4%) = 13
155 REKEY(5%) = 14
```

```
160 REKEY(6%) = 15

165 REKEY(7%) = 21

!>>> SAC MOD

!*** Add extra code to allow error traping for end of file

!*** was :- 200 INPUT LINE #1%, L$

!***

200 IF flag% <> new_sample% THEN

        WHEN ERROR IN

            INPUT LINE #1%, l$

        USE

            SELECT err

CASE 11          ! 11 is the error-code for end of file detected end_of_file%
= yes%

                CASE ELSE

                    error_flag% = yes%

            END SELECT

        END WHEN

        IF end_of_file% = yes% OR error_flag% = yes% THEN

    GOTO 29000 ! temporary end - may need to do more work here END IF

    else

        if next_date$ <> "" then

            l$ = next_date$

            next_date$ = ""

        end if

    END IF

!<<< SAC MOD

201 LDATE$ = MID$( EDIT$(L$,13%), 2%,  LEN(L$)-1% )

202 PRINT '202 ' ; LDATE$

210 INPUT LINE #1%, LTIME$ \ LTIME$ = EDIT$( LTIME$, 13% ) 211
PRINT '211 ' ; LTIME$
```

```
220 INPUT LINE #1%, BIRD$  \BIRD$  = EDIT$( BIRD$, 13% ) 221 PRINT
'221 '; BIRD$

230 INPUT LINE #1%, SEX$   \SEX$   = EDIT$( SEX$ , 13% ) 240 INPUT
LINE #1%, AGE$   \AGE$   = EDIT$( AGE$ , 13% ) 250 INPUT LINE #1%,
LOC$    \LOC$    = EDIT$( LOC$ , 13% ) 251 PRINT '251 '; LDATE$,
LTIME$, BIRD$, SEX$, AGE$, LOC$

260 INPUT LINE #1%, NEAR_BIRD$ \ NEAR_BIRD%=INTEGER(
EDIT$(NEAR_BIRD$,13%)) 270 INPUT LINE #1%, JUNK$ ! IGNORE
COMPUTER GENERATED MEANINGLESS DATA 280 PRINT LDATE$,
LTIME$, BIRD$, SEX$, AGE$, LOC$, NEAR_BIRD%

281 PRINT

300 REM next section is loop inputting activities and times into arrays 305   FOR
RZ% = 1% TO 100%

\               RA(RZ%) = -1

\               NEXT RZ%

\ !                                   set RA to 'NOT'

310 NACT% = 0%

320 NREACT% = 0%

350 FOR R% = 1% TO 100%

!>>> SAC MOD

!*** This modification allows trapping of the end-of-file, which passes control
!*** to line 640

!*** was :- 370 INPUT #1%, L$ \ L$=EDIT$( L$, 13% )

!***

370 WHEN ERROR IN

            INPUT #1%, L$

      USE

            SELECT err

CASE 11             ! error code for end of file end_of_file% = yes%

                  CASE ELSE

                        error_flag% = yes%

            END SELECT

      END WHEN

      IF error_flag% = yes% THEN
```

```
        GOTO 29000              ! program end END IF

                IF end_of_file% = yes% THEN

                        GOTO 640        ! print results

                END IF

                L$=EDIT$( L$, 13% )

!*** Modification to allow the following :-

!*** option 1 - Look for the start of a new sample ( NN/NN/NN ) - flag% = 1%
!*** option 2 - Ignore any data non-numeric                    - flag% = 0% !*** option
3 - Special cases for keycodes 17 & 18                - flag% = 2% !*** option 4 -
Special cases for keycodes REKEY(1-7)                 - flag% = 3% !*** option 5 -
Special return value for keycode noto known     - flag% = 99%

!       initalize all the constants / variables we will use

sac_initalize:

        error_flag% = no%

        flag% = 0%

!       option 1 - check for a date - indicating the start of a new sample

option1:

        date% = no%

        gosub check_1_date      ! returns date% = yes% if l$ is a date

        if date% = yes% then

                GOTO 400

        end if

!       option 2 - ignore any non-numeric data

option2:

        WHEN ERROR IN

                l% = val%( l$ )

        USE

                error_flag% = yes%

        END WHEN

!       if non-numeric end

        IF error_flag% = yes% THEN
```

```
                error_flag% = no%
non_numeric$ = l$   ! store for later on when creating whowith data
!       now read in piece of carrbage data ( might be the next date )
                when error in
                        input #1%, next_date$
                use
                        select err
                                case 11                 ! error code for end of
file
                                        end_of_file% = yes%
                                case else
                                        error_flag% = yes%
                        end select
                end when
                if error_flag% = yes% then
                        goto 29000      ! program end
                end if
                if end_of_file% = yes% then
                        goto 640        ! print results
                end if
                flag% = new_sample%             ! really are signaling the end
of this
                                                ! sample
        GOTO 400
    END IF

!       option 3 - special case for keycodes 17 & 18
option3:
    IF l% <> 17% AND l% <> 18% THEN
        GOTO option4
    END IF
```

```
        INPUT LINE #1%, state$
        state$ = EDIT$( state$, 12% )
        WHEN ERROR IN
                state% = VAL%( state$ )
        USE
PRINT "ERROR, state for keycode 17 or 18 invalid, ";state$ error_flag% = yes%
        END WHEN
        IF error_flag% = yes% THEN
                GOTO 400
        END IF
        IF state% < 0% THEN
PRINT "ERROR, state for keycode 17 or 18 negative, ";state% error_flag% =
yes%
                GOTO 400
        END IF
        diff% = state% - last_state%
        key17_18%( count%, 0% ) = last%
        key17_18%( count%, 1% ) = diff%
        count% = count% + 1%
        IF count% > key17_18_max% THEN
PRINT "key17_18%() array needs to be more than ";count% error_flag% = yes%
                GOTO 400
        END IF
        last% = 1%
        last_state% = state%
        flag% = keycode17_18%
!       was goto 400, but maybe should be goto 370
        GOTO 370
!       option 4 - special cases for keycodes REKEY(1-7)
option4:
```

```
        IF I% = 0% THEN
PRINT "Keycode 0 found,and ignored for ";LDATE$;" ";LTIME$
                PRINT
        GOTO option5            ! a zero at end of sample means nothing END IF
        LKEY(R%) = INTEGER(L$)
        INPUT #1%, L$
        L$=EDIT$( L$, 13% )
!>>>SAC MOD
!*** to allow trapping of string values when should be numeric values only when
error in
                key_time = INTEGER( L$ )
        use
                error_flag% = yes%
        end when
        if error_flag% = yes% then
error_flag% = no%               ! reset the error flag to carry on print "An error
occured trying to allocate LTIME"
print "Read record from file containing :- ";L$ print "Will ignore & continue on"
        end if
!       if any key time is less than the previous key time then ignore it, as it is
!       probably junk
        if key_time => last_key_time then
                ltime( r% ) = key_time
                last_key_time = key_time
        else
        goto 370                ! read the next line end if
!<<<SAC MOD
        NACT% = NACT% + 1%
!       is the key signifying a reactivity?
        FOR J% = 1% TO NRK%
                IF LKEY(R%) = REKEY(J%) THEN
```

```
                    NREACT% = NREACT% + 1%
                    RA(R%)  = NREACT%
                    ra_splits( r% ) = lkey( r% )
                    flag% = keycode_rekey%
                    GOTO option5
                END IF
            NEXT J%
!           leave loop as reaction code found or not reaction code
option5:
            IF flag% = 0% THEN
                flag% = keycode_unknown%
            END IF
400 IF flag% = new_sample% THEN 490
!<<< SAC MOD
480 NEXT R%
481 PRINT 'Warning : read loop ended ERROR or >DIM' \ STOP
490 ! jump to here if next line is a bird ID not an activity no. \                IF   RA(
NACT% ) > 0 THEN NREACT% = NREACT% - 1%
\           NACT% = NACT% -1%
\!
491 PRINT
\           PRINT 'R%= '; R%, 'L 491'
\           PRINT 'FINISHED' ,  NACT%, 'ACTIVITIES  OF  BIRD' , BIRD$
\           PRINT '       ' , NREACT%, 'REACTIONs  FOR BIRD' , BIRD$
\           PRINT
600 ! now get reactor data
605 NRD% = 0%
606 SPQ% = 2%
610 IF NREACT% = 0 THEN 720 ELSE 630 ! no codes needed
!>>>SAC MOD
```

```
!*** change references to l$ to non_numeric$
620 when error in
                    input line #1%, non_numeric$
               use
                    select err
case 11             ! error code for end of file end_of_file% = yes%
                         case else
                              error_flag% = yes%
                    end select
               end when
          if error_flag% = yes% then
               goto 29000     ! program end
          end if
          if end_of_file% = yes% then
               goto 640       ! print results
          end if
          non_numeric$ = EDIT$( non_numeric$, 13%)
! now read in piece of carrbage data ( might be the next date ) when error in
               input #1%, next_date$
          use
               select err
                    case 11        ! error code for end of file
                         end_of_file% = yes%
                    case else
                         error_flag% = yes%
               end select
          end when
          if error_flag% = yes% then
               goto 29000     ! program end
          end if
```

```
        if end_of_file% = yes% then
            goto 640        ! print results
        end if
        flag% = new_sample%         ! really are signaling the end of this
                                    ! sample
!<<<SAC MOD
630 NRD% = NRD% + 1%
!>>> SAC MOD
!*** Line 631 has been commented out to stop the reading of LDATE$, which will
!*** be handeled at line 990
!*** was :- 631 INPUT LINE #1%, G$ REM  IGNORE AS GARBAGE....
!***
!<<< SAC MOD
!>>> SAC MOD
!*** All the following lines have been ammended to use the correct value !***
NON_NUMERIC$ (not L$ )
640 PRINT non_numeric$
650 IF SPQ% = 0% THEN 660
651 INPUT 'NO OF SPLITS <0 OR 2>', NSP%
655 ON NSP% + 1% GOTO 658, 690, 680 OTHERWISE 690 658 SPQ% = 0%
!>>> SAC MOD
! indicate that nrd% is a 0 split not a 2 split
who_splits%( nrd%, 0 ) = 0
!<<< SAC MOD
660 WHO_WITH$( NRD% ) = non_numeric$
675 GOTO 700
680 INPUT 'POSITIONS OF 2 SPLITS <S1,S2>', SP1%, SP2%
!>>> SAC MOD
! indicate that nrd% is a 2 split not a 0 split
who_splits%( nrd%, 0 ) = 2
!<<< SAC MOD
```

```
681 WHO_WITH$(NRD%) = MID$( non_numeric$, 1%, SP1% - 1%)

\       PRINT WHO_WITH$(NRD%)

682 WHO_START$(NRD%) = MID$( non_numeric$, SP1%, SP2% - SP1%)

\       PRINT WHO_WITH$(NRD%), WHO_START$(NRD%)

\       PRINT LEN( non_numeric$ ), SP2%, LEN( non_numeric$ ) -SP2% + 1

683 WHO_WON$(NRD%) = MID$( non_numeric$, SP2%, (LEN( non_numeric$) - SP2% + 1%) )\ PRINT WHO_WITH$(NRD%), WHO_START$(NRD%), WHO_WON$(NRD%)

686 INPUT 'IS THIS OK <Y,N>?', QOK$

688 IF EDIT$(QOK$, 47%) = 'N' THEN 680 ELSE 700

689 ! end of double split

690 PRINT 'ILLEGAL REPLY! TRY AGAIN . . . .'

691 GOTO 651

!<<< SAC MOD

! is this the last reaction coding?

700 IF NRD% < NREACT% THEN 620

702 !>>> SAC MOD

! extra routine to ignore any information after the reactivies until a DATE ! is found
- hopefully won't loose anything ***

        date% = no%

        temp_l$ = l$                    ! store so not overwritten

        l$ = next_date$

gosub check_l_date              ! returns date% = yes% if l$ is a date

        l$ = temp_l$                    ! restore contents of l$

        if date% <> yes% then

! now read in piece of carrbage data ( might be the next date )

                        when error in

                                input #1%, next_date$

                        use

                                select err

case 11                 ! error code for end of file
```

```
                                        end_of_file% = yes%
                                    case else
                                        error_flag% = yes%
                                end select
                            end when
                            if error_flag% = yes% then
                                goto 29000              ! program end
                            end if
                            if end_of_file% = yes% then
                                goto 720                ! print results
                            end if
                            goto 702
                    end if
                    !<<< SAC MOD
720 ! now process times
!>>> SAC MOD
!*** This line was changed to set the default value to 300 if <RETURN> only !***
was pressed. Before this would have been 0.
!*** was :- 730 INPUT 'TIME stopped at < 300 > ', LTIME( NACT% + 1% )
!***
730 INPUT 'TIME stopped at < 300 > ', temp%
                    IF temp% = 0% THEN
                        temp% = 300%
                    END IF
                    LTIME( NACT% + 1% ) = temp%
!<<< SAC MOD
800 !  NOW PRINT TO OUTPUT FILE
801 PRLN_A1$=\    \!\        \\    \\    \\    \' 802 PRLN_A2$='### ##
#### '
803 PRLN_A3$=\     \'
804 PRINT PRLN_A1$;PRLN_A2$;PRLN_A3$ \PRINT
```

```
805 PRINT '      1      2      3      4      5      6'\          PRINT
'12345678901234567890123456789012345678901234567890123456789012345678901234567890'

\               PRINT BIRD$

\               PRINT SEX$

\               PRINT AGE$

\               PRINT LOC$

\               PRINT LDATE$

\               PRINT LTIME$

\               PRINT

\!

810 FOR P% = 1% TO NACT%

8 2 0                          P R I N T          # 5 %          U S I N G
PRLN_A1$,BIRD$,SEX$,AGE$,LOC$,LDATE$,LTIME$;

830   PRINT #5% USING PRLN_A2$,near_bird%,LKEY( P% ),LTIME(
P%+1%)-LTIME( P% ); 840 IF RA( P% ) > 0 THEN 850 ELSE 870

!>>> SAC MOD

! addition to allow (hopefully) 6,7,8 and 13,14,15 reactivities to be output !
correctly

! was 850 PRINT #5% USING PRLN_A3$, WHO_WITH$( RA( P% ) ) ;

! was\   PRINT #5% USING PRLN_A3$, WHO_START$( RA( P% ) ) ; ! was\
PRINT #5% USING PRLN_A3$, WHO_WON$(   RA( P% ) ) ! was\   GOTO
880

!

850 select ra_splits( p% )

                        case 6,7,8

                                check% = 1%

                                found_key_reactivity% = no%

while ( check% <= nrd% ) and ( found_key_reactivity% = no% )

! if we've found the correct reactivity for a key code

                                        if ( who_splits%(check%,0) = 2 ) and (
who_splits%(check%,1) = 0) then ! set a flag to show this has been used

                                                who_splits%( check%, 1) = 1
```

```
print #5% using prln_a3$, who_with$( check% ) ; print #5% using prln_a3$, who_start$( check% ) ; print #5% using prln_a3$, who_won$( check% ) found_key_reactivity% = yes%
                                        end if
                                        check% = check% + 1
                                    next                ! when
                                    if found_key_reactivity% = no% then
print "Error - NO reactivty found for 6-8 keycode"
print #5%,"Program Error - KEYPRESS/REACTIVITY for keys 6-8"
                                        end if
                                case 13,14,15,21
                                        check% = 1%
                                        found_key_reactivity% = no%
while ( check% <= nrd% ) and ( found_key_reactivity% = no% )
! if we've found the correct reactivity for a key code
                                        if ( who_splits%(check%,0) = 0 ) and ( who_splits%(check%,1) = 0) then ! set a flag to show this has been used
                                                who_splits%( check%, 1) = 1
print #5% using prln_a3$, who_with$( check% ) found_key_reactivity% = yes%
                                        end if
                                        check% = check% + 1
                                    next                ! when
                                    if found_key_reactivity% = no% then
                                        print "Error - NO reactivty found for 13-15 keycode"
                                        print #5%,"Program Error - KEYPRESS/REACTIVITY for keys 13-15"
                                        end if
                                case else
print "Error - couldnt find a reactivity code when allocating who_xxx" print "for keypresses 6-8,13-15,21"
                                    print #5%,"Program Error - KEYPRESS/REACTIVITY"
```

```
        end select
        goto 880
!<<< SAC MOD
870  PRINT # 5%   \! NEW LINE ON FILE
880  NEXT  P%
!>>> SAC MOD
!        *** for keycode/reactivity problem
for n% = 1% to 50%
who_splits%( n%, 0 ) = 0 who_splits%( n%, 1 ) = 0
        ra_splits( n% ) = 0
        ra_splits( n% + 50% ) = 0
next n%
!<<< SAC MOD
!>>> SAC MOD
!*** Addtion to allow keypress 17 & 18 to be output
!***
900 key17_18%( count%, 0% ) = last%        !{ setup remaining
                key17_18%( count%, 1% ) = 300% - last_state%     !{   keypress
difference
                FOR n% = 1% TO count%     ! don't print the first
                ! values ( where n%=0 ) PRINT #5% USING
PRLN_A1$,BIRD$,SEX$,AGE$,LOC$,LDATE$,LTIME$;
        PRINT #5% using prln_a2$,near_bird%,key17_18%( n%,0%
),key17_18%( n%,1% ) NEXT n%
                last% = 0%
                last_state% = 0%
                count% = 0%
                last_key_time = -9
!<<< SAC MOD
!>>> SAC MOD
!*** Program was stopping at end of first sample as it reached the stop
```

```
!*** statement on line 990. This has been changed to go to line 200 to get the !***
LDATE$ again

!*** was :- 990  STOP

!***

990 GOTO 200

!

!

!       SUBROUTINE to check contents of l$ is a valid date

!

check_1_date:

        if len( l$ ) < 8% then

                goto check_1_date_end

        end if

        rubbish$ = MID$( l$, 1%, 1% )

        month$          = MID$( l$, 2%, 2% )

        sep1$   = MID$( l$, 4%, 1% )

        day$    = MID$( l$, 5%, 2% )

        sep2$   = MID$( l$, 7%, 1% )

        year$   = MID$( l$, 8%, 2% )

!       if no / then cannot be a date (start of new sample)

        IF sep1$ <> "/" AND sep2$ <> "/" THEN

                GOTO check_1_date_end

        END IF

!       setup error trap. If any of the day$,month$,years$ varaibles contain

!       characters this will cause an error trap. This is a good way to find out if

!       a variable contains characters

        WHEN ERROR IN

                day%   = VAL%( day$ )

                month% = VAL%( month$ )

                year%  = VAL%( year$ )
```

```
        USE
                error_flag% = yes%
        END WHEN
!       if day, month or year contains ascii characters then try next option
        IF error_flag% = yes% THEN
                GOTO sac_date_err
        END IF
!       check date values are allowable
        IF day% < 1% OR day% > 31% THEN
                GOTO sac_date_err
        ELSE
                IF month% < 1% OR month% > 12% THEN
                        GOTO sac_date_err
                ELSE
                        IF year% < 1% OR year% > 99% THEN
                                GOTO sac_date_err
                        END IF
                END IF
        END IF
!       have found start of a new sample
        flag% = new_sample%
        date% = yes%
        goto check_1_date_end
!       date error routine
sac_date_err:
        PRINT "Found date separators - /"
PRINT "But there was something wrong with the date values"
        PRINT "Date is ";l$
        PRINT
check_1_date_end:
```

```
        return
29000 CLOSE #1
                CLOSE #5
                END
```

Appendix 3

BASIC programme for calculating the multiple-comparisons post-hoc test of the Kruskal-Wallis one-way analysis of variance

```
 10 REM Programmed by AS Adikherana and DJ Halley

100 CLS:KEY OFF

110 DIM D(20),CD(20,20),MEAN(20),MC(20,20)

120 PRINT:PRINT

130 PRINT TAB(5);"Enter filename for result : ";:INPUT "  ",NAMA$

140 FILENAME$=NAMA$+".doc"

150 '

160 PRINT TAB(5);"Enter z-value = ";:INPUT " ",Z

170 PRINT

180 PRINT TAB(5);"How many categories ";:INPUT "? ",N

190 PRINT

200 SUM=0

210 FOR I=1 TO N

220      PRINT TAB(5);"Number of cases in ";I;:INPUT " = ",D(I)
```

```
230     SUM=SUM+D(I)

240 NEXT I

250 '

260 PRINT

270 FOR I=1 TO N

280     PRINT TAB(5);"Enter mean rank value of Category ";I;:INPUT " =
",MEAN(I)

290 NEXT I

300 '

310 FOR I=1 TO N-1

320     FOR J=I+1 TO N

330       MC(I,J)=ABS(MEAN(I)-MEAN(J))

340     NEXT J

350 NEXT I

360 '

370 FOR I=1 TO N-1

380     FOR J=I+1 TO N

390       CD(I,J)=1/D(I)+1/D(J)

400     NEXT J

410 NEXT I

420 '
```

```
430 PRINT
440 FOR I=1 TO N-1
450     FOR J=I+1 TO N
460       CD(I,J)=SQR((SUM*(SUM+1)/12)*CD(I,J))
470     NEXT J
480 NEXT I
490 '
500 FOR I=1 TO N-1
510     FOR J=I+1 TO N
520       CD(I,J)=Z*CD(I,J)
530     NEXT J
540 NEXT I
550 '   finito
560 OPEN FILENAME$ FOR OUTPUT AS #1
570 FOR I=1 TO N-1
580     FOR J=I+1 TO N
590       PRINT #1," Value of Comparison between ";I;" and ";J;" = ";CD(I,J);
600       PRINT #1,"   Diff. Mean Rank = ";MC(I,J)
610     NEXT J:PRINT #1,"  "
620 NEXT I
```

```
630 '
640 FOR I=1 TO N-1
650     FOR J=I+1 TO N
660       IF MC(I,J)=>CD(I,J) THEN 670 ELSE 690
670       PRINT #1,"Case ";I;" vs. ";J;" --  significant at z = ";Z
680       GOTO 700
690       PRINT #1,"Case ";I;" vs. ";J;" --  not significant at z = ";Z
700     NEXT J:PRINT #1,"  "
710 NEXT I
720 CLOSE #1
730 END
```

Appendix 4

Reprint of Halley, D.J. (1992): Population changes and territorial distribution of common buzzards *Buteo buteo* in the central highlands, Scotland. Bird Study 39.

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Bird Study (1992) **39**, 000–000

Population changes and territorial distribution of Common Buzzards *Buteo buteo* in the Central Highlands, Scotland

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The population of Common Buzzard in a 94 km² area of upper Strathspey, Scotland, increased from 14 to 22 adult pairs between 1971 and 1988–89. Territory size was not significantly different between the two dates. Territory size was unaffected by absolute length or proportion of boundary shared with other pairs, but was positively correlated with the proportion of thickest stage conifer plantation enclosed. Habitat strongly influenced territorial distribution.

Common Buzzards *Buteo buteo* and the closely related Red Tailed Hawk *B. jamaicensis* of North America exhibit a very plastic range of territorial organization, from small defended ranges with a large communal hunting area[1,2] to exclusive territories,[1] and from completely migratory to completely sedentary populations, in which territoriality may be seasonal or year round. Both species are catholic in their habitat choice, from treeless steppe and moorland to heavily forested regions.[4–7] See Cramp[8] for an overview for *B. buteo*.

Theoretical discussion has concentrated on the role of ecological factors, such as food supply, in relation to social factors such as population pressure, intruder frequency, and economic defensibility, in determining territory location and size.[9–14] This paper describes an investigation into the roles of habitat and population size on the siting and size of breeding territories in a sedentary, territorial population of Common Buzzards. Distribution in 1988–89 is compared with data from, 1968–1972 (in particular 1971) collected by Weir & Picozzi.[3]

METHODS

The study area was a 94 km² section of upper Strathspey, Highland Region, Scotland, including a 10-km stretch of the main Strath (valley) floor and 2 main side glens. The valley runs from south west to north east. Upper slopes are dominated by heather moor, with areas of planted conifer woodland. Lower slopes are covered by a mix of birch woodland, meadow, conifer plantation and moorland. A little land is cultivated on the lowest slopes. The flat bottom of the valley is occupied by the Insh Marshes, which are frequently flooded and dominated by sedge and rough grasses, and by Loch Insh, a 3-km² valley lake. The natural history of the region has been described.[15]

The valley floor lies at c. 220 m elevation. The climate is temperate; summers are cool and winters severe by British standards with an average of 103 days of frost and 35 days of snow annually on the valley floor. Precipitation is distributed through the year, averaging c. 900 mm.[16] Buzzards recolonized the study area after local extinction from 1945 onwards. Extensive population studies were carried out in 1968–1972 by Weir & Picozzi.[1,17–20] In conformity with their work, the upper limit of the study area was set at the 380 m contour, above which buzzards ranged only marginally and did not nest. The study area corresponds exactly with the south western portion that of Weir & Picozzi,[3] except for one side glen which they excluded. However, territorial buzzards

were known to be absent from this glen during their study so the validity of comparisons made is unaffected (D. Weir, pers. comm.).

Fieldwork was carried out between January 1988 and April 1989. Territorial ranges were mapped as in the previous study:[3] displays, boundary disputes, perching posts, and general movements were recorded for each pair on 1:25000 Ordnance Survey maps throughout the study period. The final boundary was drawn as a minimal polygon around all recorded observations (repeat sightings in the same location were not recorded), with amendments where data (e.g. on boundary disputes) delineated boundaries more clearly.

The study area was classified into 14 ground cover types based on Ordnance Survey 1:25000 maps and thorough ground survey (Table 1). These data were compiled on a PLUTO graphics computer to prepare a false colour map of the area at a scale of 18.5 pixels/hectare. Accuracy was checked against sample areas from original maps. Territorial boundaries were superimposed and the resulting representation used in a log-linear analysis of territorial distribution in relation to habitat. To allow for error in mapping transcription (photographically from the original map to the digital PLUTO false colour map), the count of pixels in each category was divided by 10 for the purposes of calculation.

Significance levels are expressions of the probability that a given result is the product of a genuine difference in populations. The conventional threshold for concluding a significant effect, $P < 0.05$, implies that there is less than once chance in 20 of finding a significant effect when there is none (a Type 1 Error). Where repeated tests are carried out, the chances of producing a Type 1 Error increase. In order to correct for this, Bonferroni's Procedure can be applied.[21] This involves partitioning the usual significance level. Where there is no prior reason for partitioning unequally, the procedure reduces to an equal division of the significance level between all

Table 1. Log-linear analysis of territorial composition

	*Observed count**	*Expected count*	*Adjusted residual*	*Significant at P < 0.003†*	
				+	−
Habitat					
Birchwood	1215	613	32·3	Yes	
Seedling Pinewood	59	66	−1.1		
Thicket Pinewood	1309	1918	−20.9		Yes
Mature Pinewood	119	76	6.2	Yes	
Natural Pinewood	87	97	−1.3		
Underplanted Birch	104	39	13.2	Yes	
Oakwood	101	41	12.0	Yes	
Mixed Woodland	18	8	4.6	Yes	
Marsh	76	476	−24.1		Yes
Water	147	310	−12.0		Yes
Rough Pasture	1108	640	24.7	Yes	
Cultivation	814	469	20.9	Yes	
Moorland	1359	1720	−12.8		Yes
Urban	11	54	−7.4		Yes

*See Methods.

†Bonferroni's correction applied to significance levels to adjust for repeated tests (see Methods). A significant positive effect (+) indicates that the habitat type was over-represented within buzzard territories as compared with the study area as a whole; a significant negative effect (−) indicates under-representation.

tests. In the present case with 14 comparisons (Table 1), 0.05/14 = 0.00357, which can be conservatively approximated as 0.003.

RESULTS

Population

Fourteen pairs of Buzzard were recorded within the study area in 1971,[3] considered the best mapped year of the earlier study (Weir, pers. comm.) (Fig. 1). The population increased by 57% to 22 pairs in 1988–89 (Fig. 2). Buzzard territories covered 37% of the study area.

Territory size

Territory size ranged from 38–319 ha, mean = 179 ha+84.8 SD, median 165.5 ha. These figures match closely, and do not differ significantly, from the figures obtained for the same area in 1971 (Mann–Whitney *U*-test, $P > 0.05$): range 26–387 ha, mean 190.5+109.5 sd, median 180.5 ha (Fig. 3). In contrast, the cumulative territory sizes calculated for the whole of the 1968–72 study period were much larger than those in 1988: range 298–929 ha, mean 475 ha+176.6 sd, median 446 ha[3]. This difference is highly significant (Mann–Whitney, $P < 0.0001$).

The sizes of the two smallest ranges recorded in the present study (21 & 22) were undoubtedly underestimated. Adult pairs were present in both cases and bred in at least one, but sightings were few (5 and 7, respectively) and exclusively of birds flying from the nest (or close by) or circling around the nest wood while alarm-calling. Other territory sizes were based on a minimum of 20 material observations (observations which were not repeats of birds in the same location) (Fig. 3). All included territorial behaviours and observations outwith the breeding season. The number of observations tended to be higher in the southeast of the study area, where I lived, and where (unpublished) behavioural studies were made. Nevertheless, territory size is not correlated with number of observations ($r = 0.115$, $P > 0.05$). The number of observations was not significantly correlated with proportion, or area, of thicket stage woodland within the territory ($r = -0.198$ and $r = -0.095$ respectively; $P > 0.05$ in each case). Territories 21 and 22 have been excluded from all further analyses.

Territory size was positively correlated with proportion of thicket stage conifer plantation

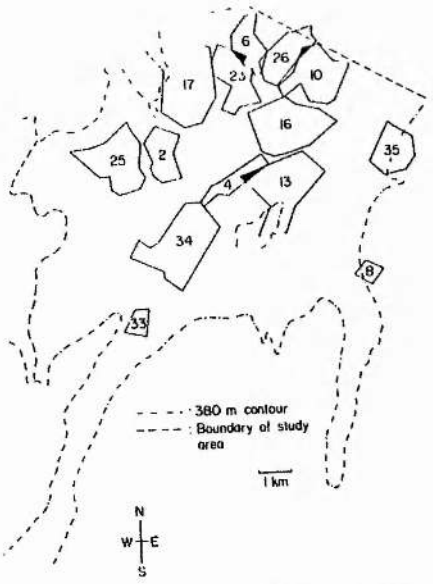

Figure 1. Territorial distribution in 1971.

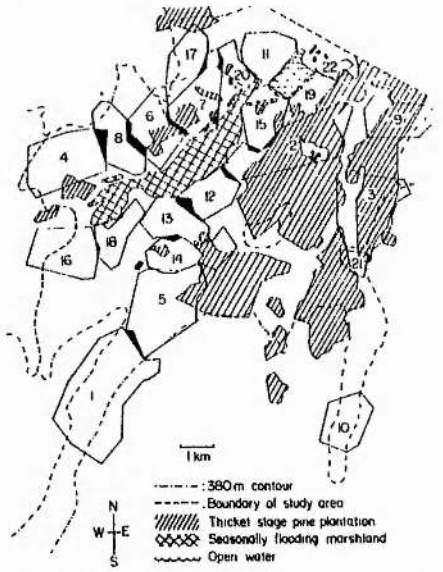

Figure 2. Territorial distribution in 1988–89 in relation to thicket stage pine plantations, seasonally flooding marshland, and open water.

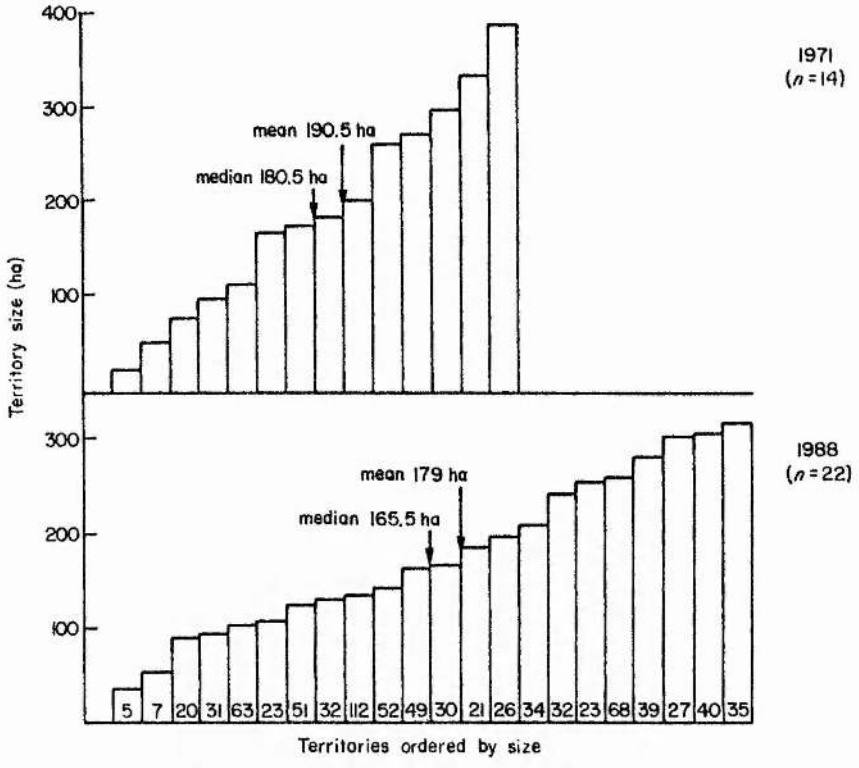

Figure 3. Territories ordered by size. Numbers 1988–89 indicate the number of material observations (see Methods).

contained ($r = 0.446$; $t = 2.17$, $P < 0.05$). No significant relationship was found between territory size and any other habitat variable, or between territory size and extent above 380 m. The latter result is in contrast to findings for the same population in 1968–72.[3]

No significant relationship was found between either the territory size and the proportion, or length, of shared territorial boundaries (Spearman's Rho, $P > 0.05$ in each case).

Dispersion and habitat selectivity

If habitat was unimportant in determining the dispersion of buzzard territories, it would be expected that each habitat type would be included within territories roughly in line with its frequency within the study area as a whole. However, analysis of the habitat structure indicated that, of the 14 habitat types, 7 were significantly over represented and 5 significantly under represented within territories. Significant over-representation was shown for birchwoods, rough pasture, cultivations, birchwoods underplanted with pine, oakwoods and mature pine plantations in that order (but see Discussion). Marshland, thicket stage pine plantations, moorland, open water, and built-up areas were significantly underrepresented. In all cases results were highly significant, despite the conservative procedures used in the analysis (see Methods). Excluding marshland and water from the analysis (almost unused and unusable habitats, respectively) did not materially alter the results for the remaining habitat types.

DISCUSSION

Several factors may account for the population increase from 14 pairs in 1968–72 to 22 pairs in 1988–89. Continuing natural increase follow-

ing recolonisation in 1945, relaxation in illegal persecution, and/or an increase in the carrying capacity of the area are all possibilities. Poisoning of buzzards was one of the most common causes of mortality in the earlier period (D. Weir, pers. comm. and Ref. 18); levels of persecution appear to have much reduced since. Several of the gaps in distribution in 1971, now occupied by buzzard territories, correspond to estates which practised raptor control at that time (D. Weir, pers. comm.).

The previous study's survey techniques were used in order to preserve as much comparability between the studies as possible.[3] Their caveats as to the adequacy of the mapping techniques also apply to this work. In particular, although territorial overlaps recorded were small (1.6% of the total territorial area), some at least of this figure was due to records of high soaring birds. As Gargett[22] noted for Verreaux's Eagle *Aquila verreauxi*, soaring range is often somewhat wider than ground range; similarly display and hunting ranges may not be identical in buzzards.

Territorial boundaries appeared to be extremely closely defined where contested, but much more vague when bounding unoccupied ground. This may, however, have been an artefact of the scarcity of territory-marking behaviours along such boundaries; territory sizes may be slightly overestimated as a result.

The present study found similar territory sizes to those in 1971, considered the best mapped year of the earlier study (D. Weir, pers. comm.). However, their cumulative distributions for 1968–72 are significantly larger. Weir & Picozzi considered that the discrepancy between the data collected for individual years and the cumalative total represented mapping deficiencies in each individual year, through territorial boundaries may have shifted somewhat from year to year.

The present study suggests that other interpretations are possible. Average territorial sizes as mapped in a single year were remarkably constant despite a 17-year interval and a 57% increase in population (Figs 1 & 2). At the same time the central valley has become almost completely occupied by territorial adults, and much of the more marginal upper ground and side glens colonized. In contrast to the earlier study, there is little room for territories in the main valley to shift. In the earlier study, birds were not so constrained; the population was still recolonizing Speyside from re-establishment in 1945, and much unoccupied ground remained. In this situation, territories containing a sufficient food base might have shifted from year to year over the large pool of unoccupied ground.

Weir & Picozzi's yearly maps may therefore (contrary to their belief) have been good representations of territories at that time, the much smaller population permitting a more fluid shifting of boundaries than is the case with a population where territories frequently abut one another directly. This interpretation would reconcile the exclusive nature of territorial defence characteristic of this population with the large range size and extensive overlaps noted.[3]

If true, this interpretation of the data has implications for theories of territoriality, in particular indicating that territory sizes may be influenced more by asocial criteria than social factors such as defence costs.[13,14] The findings that the proportion of territory boundary that is contested does not affect territory size is consistent with this argument. The most important criterion may be food availability. Dare[23] considered that buzzard territories contained a definite (unquantified) food value. Weir & Picozzi[3] (but not the present study) found that territories extending above 380 m into low-productivity moorland were larger. In this study, area of thicket pine plantation, an almost barren habitat in terms of prey availability, was found to be significantly correlated with territory size.

There appeared to be no tendency to abandon upper elevations of territories in winter in 1988–89, in contrast to 1968–72.[3] The reason for this difference in observations is unclear, though it may be related to the weather: the 1987–88 winter was relatively mild, and the 1988–89 winter the mildest on record (since 1820). However, one territory (Territory 1) was abandoned outright over winter. This territory was the highest in average elevation, and rabbits and sheep (carrion) were absent, in contrast with all other territories. Winter abandonment of territories with poor food supplies has been found elsewhere (e.g. in the New Forest, England[2]).

Buzzards showed marked biases in the habitat types included within territories. This

pattern is probably related ultimately to prey availability. However, in 1968–72 territories often included extensive marshland areas[3] (e.g. Territories 2, 23, 25 in Fig. 2), a habitat almost entirely absent from territories in 1988–89 through their boundaries often followed its edge closely. Hen Harriers *Circus cyaneus* may be a factor in this change, through competitive exclusion and/or intraspecific territoriality. Harriers have increased greatly in numbers locally in the last two decades with *c.* 15 individuals at a communal roost on the marsh in 1988–89; only occasional birds occurred in 1968–72 (Z. Bhatia, pers. comm.). Interspecific territoriality against *Buteo* species occurs in wintering populations of Hen Harriers in North America.[24] However, in the present study immature Buzzards did hunt, and sometimes held feeding territories, on the marsh where sufficient perching posts occurred.

Habitats over-represented within territories included mature woodland of all types and cultivated and grazing land. However, three of these habitats (oakwood, cultivation, and mature pinewood) were both small in total area and occur as fragments in areas of other preferred habitats. They may be passively included in territories because of this. However, the only area of mixed mature woodland occurred on an island in Loch Insh at the edge of Territory 11. Birds actively flew to this site so that passive incorporation can be excluded as an explanation for the apparent preference. In the study area all the preferred habitats are associated in a mosaic of relatively small, interspersed blocks typical of the conditions under which Buzzards breed at highest densities elsewhere in Britain (e.g. Wales[11] and Devon[2]).

A well documented change in vegetation over the period between this study and that of 1968–72 has been the great increase in extent of thicket stage conifer plantations, particularly at higher elevations. Conifer plantations at this stage of growth have been found to restrict buzzard and other raptor populations elsewhere in Britain,[11,25] but re-establishment of buzzards takes place as the forests reach maturity (Ratcliffe quoted in Newton, Davis & Davis[11]). In the present study also, birds avoided thicket stage plantations, and territory size was postively related to extent of thicket stage afforestation. The only buzzard territory occupied in 1968–72 from which birds are now absent (Territory 13, Fig. 2) has been almost completely afforested in the intervening period. In Mid-Wales traditional sites disappeared when a threshold of > 80% of land within 1 km of the nest site was covered with thicket plantation.[11] The data do not indicate whether territorial expansion took place as the amount of thicket stage plantation expanded below this threshold, as the present study would suggest.

The extent of this type and stage of afforestation would seem to be the major factor constraining range and population levels in the study area. Recent plantings of conifers have been of comparatively small scale, perhaps because most suitable land has already been planted, and because of tax changes reducing the value of forestry investments. If further plantings remain restricted, the buzzard population will presumably increase in succeeding decades as the current large areas of thicket plantation reach maturity.

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Appendix 5

Preprint of Harris, M.P., Halley, D.J. & Wanless, S. (*in press*): The post-fledging survival of young guillemots *Uria aalge* in relation to hatching date and weight. Ibis.

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The post-fledging survival of young Guillemots *Uria aalge* in relation to hatching date and growth

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The post-fledging survival of a total of 1277 young Guillemots *Uria aalge* ringed in 6 years was assessed using sightings of 267 individuals back at the natal colony and recoveries of 46 ringed birds. In two years there was a significant decline in survival prospects with estimated hatching date: the first time such a trend has been demonstrated in the Alcidae. In these years pairs breeding early had a 2–3 times greater chance of having a young survive to return to the colony than pairs breeding three weeks later. Hatching date had no effect on survival prospects in the other four seasons and in none of the years did chick body condition have a demonstrable effect on post-fledging survival.

Several studies of a range of bird species have demonstrated that young which came from eggs laid early in the season and/or were heavier at fledging, subsequently survived better than late or light young, e.g. Great Tit *Parus major* (Perrins 1965), Pied Flycatcher *Ficedula hypoleuca* (von Haartman 1967), Herring Gull *Larus argentatus* (Nisbet & Drury 1972), Manx Shearwater *Puffinus puffinus* (Perrins, Harris & Britton 1973), Cape Gannet *Sula capensis* (Jarvis 1974), Sparrowhawk *Accipiter nisus* (Newton & Marquiss 1984). Such findings give strong support to Lack's (1954) contention that birds rear young at the best time of year. However, in contrast, none of three published studies on Alcidae – the Guillemot *Uria aalge* (Hedgren 1981), Razorbill *Alca torda* (Lloyd 1979) and Puffin *Fratercula arctica* (Harris & Rothery 1985 – detected any such relationships.

The aim of this study was to determine whether hatching date or weight had an effect on post-fledging survival of 6 cohorts of young Guillemots from the Isle of May, Firth of Forth, Scotland. The study spanned a period when the breeding population stabilized and then declined after a phase of rapid increase, changes which have been attributed to a reduced level of recruitment (Harris & Wanless 1988, Halley unpublished). A positive effect of early breeding data on post-fledging survival is documented for the first time in the Alcidae.

METHODS

Each year from 1983 to 1988 samples of young Guillemots were marked in accessible parts of the colony with rings which could be read easily at a distance of up to 50 m with a ×60 telescope. Most birds were also given a plain or engraved colour-ring to aid subsequent identification. The wing-length of each chick was measured (to the nearest 1-mm from the bend of wing to the tip of the largest primary covert) and most young were also weighed (nearest 1-g). In all, 1277 chicks were ringed and measured with the annual totals varying from 132 to 276 (Table 1). Searches were made for these birds on most days during each breeding season 1984–91 and 267 (24%) were found alive at the colony when 2 or more years old. In addition 46 were reported dead elsewhere when more than 6 months old. The peak mortality of young Guillemots occurs in the autumn and early winter following fledging (Birkhead 1974, Bayer, Lowe & Loeffel 1991). Therefore, for convenience, we consider birds alive after the 1 January of the calendar year following ringing to have 'survived' and term these chicks 'survivors'; young which were never recorded again are referred to as 'non-survivors'. All analyses (below) were repeated after redefining survivors as birds known to be alive after 2 years. This had no effect on any of the findings so only results from the larger data set are reported here.

The rate of increase of wing-length does not appear to be influenced by nutrition during the time that a young bird is in the colony and is linearly related to age (Gaston 1985), so we estimated the hatching date of each chick using the relationship:

Age (days) =

0.373 ± s.e. 0.023 (wing-length, mm) − 5.8 (R^2 = 78%)

which we obtained from single measurements of 73 chicks whose hatching date was known exactly.

Within-year trends in the proportions of chicks surviving after fledging were determined using linear regression, giving each bird equal weight after grouping hatching dates into 4-day periods. Periods when fewer than ten chicks hatched were excluded. During the 6 years the annual percentage of

chicks hatched that died between hatching and leaving the colony varied from 4% to 11%, and 60% of these losses occurred in the first 9 days of life (Harris & Wanless 1988, updated). The average age at ringing for chicks in the study was 10 days. In 1984, 1985 and 1988 the age at ringing of late hatching chicks was significantly less than that of early hatching chicks (linear regressions, r-values all $P<0.001$) so these young might have had a higher chance of dying before leaving the colony. We therefore repeated all the analyses using the extreme asssumption that all the losses in any year were borne by the chicks in the last two 4-day hatching periods. This did not change any of the results (or probability levels of statistical tests) presented later.

In the 10 days after hatching a young Guillemot gains weight rapidly, the rate then declines markedly so that by the time it leaves (aged 18–23 days) the weight of an individual is more or less constant. As breeding Guillemots are intolerant of disturbance (Harris & Wanless 1984, Hatchwell 1989), we did not try to measure the growth rate of individual chicks but instead constructed a composite growth curve of weight against wing-length for each year, using a single weighing for each chick handled (Fig. 1). Linear regression analysis (initially using both untransformed and transformed data) showed that the best fit was given by the transformation -1/wing-length. The slopes and intercepts of the lines for survivors and non-survivors and between year differences were compared using analysis of covariance (ANCOVA).

To investigate whether survival of the very heaviest or lightest chicks was markedly different, we compared the observed frequency of survivors and non-survivors in the 10% of young with both the highest and the lowest condition indices (taken as observed/predicted weight from the regres-

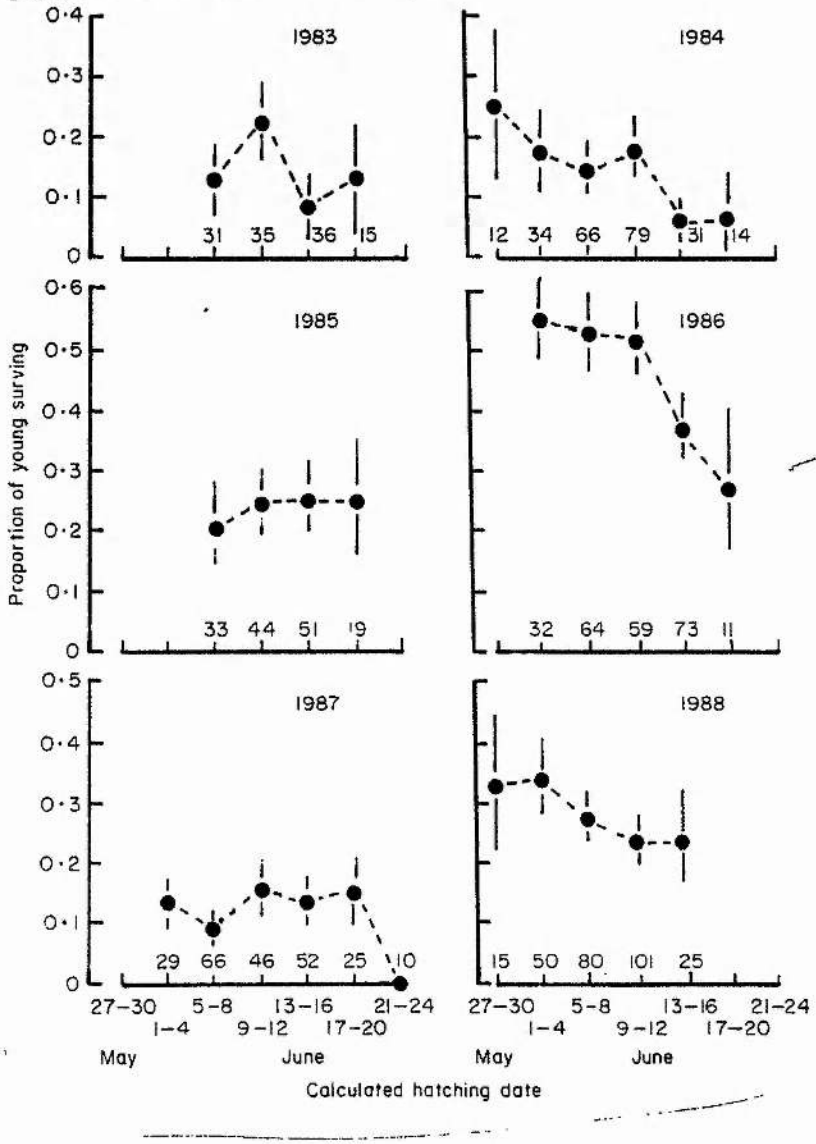

Figure 1. Plots of weight against wing-length for young Guillemots known to have survived more than 6 months (●) and those not seen again (○) in (a) 1985 and (b) 1988.

sion line of weight against transformed wing-length), with that expected from the average survival rate for that year using Fisher's exact test.

Data for each years cohort were kept separate because (a) annual recovery and resighting rates varied considerably, apparently due to differential survival (Harris & Bailey in press, D. Halley unpubl.), and (b) the young were ringed in the same areas each year so data for different years were not strictly independent.

Table 1. *Number of young Guillemots ringed on the Isle of May in 1983–88 known to survive to the following 1 January*

Year	Ringed, *n*	Reported, *n* (%)
1983	132	21 (16)
1984	241	37 (15)
1985	149	36 (24)
1986	242	114 (47)
1987	237	28 (12)
1988	276	77 (28)

RESULTS

Survival

The percentage of each cohort of ringed young known to survive more than 6 months showed considerable annual variation, ranging from 12% in 1987 to 47% in 1986 (Table 1). Inter-year comparisons in survival must be used with caution as the figures will be subject to errors associated with annual differences in resighting effort and differences in the number of years that members of each cohort were at risk of being resighted in the colony or recovered dead. Because of these potential errors we did not use statistical tests to compare survival rates between cohorts. It does, however, seem clear that young from 1986 survived particularly well. The same seems likely for the 1988 cohort since 28% were recorded again, despite records only being available for three subsequent years.

Survival in relation to hatching date

Survival of young declined significantly with hatching date in 1986 and 1988. There was also a decline in 1984 but the

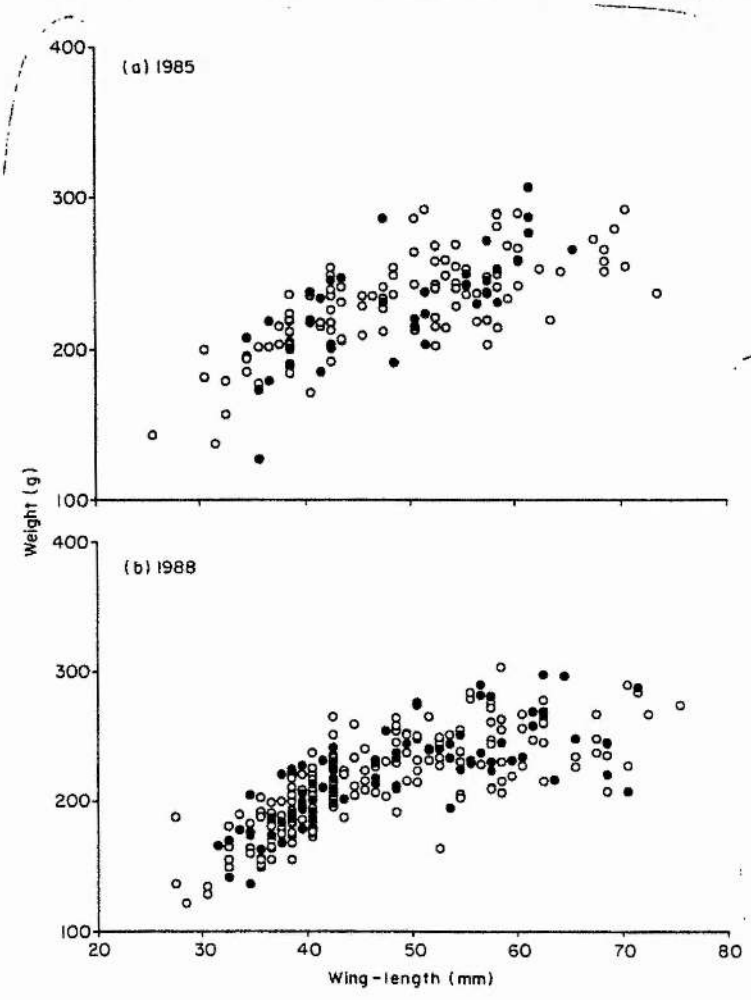

Figure 2. The change in survival with estimated hatching date of young Guillemots in 1983–88. The mean (±1 s.e.) and sample sizes for each 4-day period are shown. Significance values for the trends are given in Table 2.

Table 2. *Trends in survival of young Guillemots in relation to estimated hatching date in 1983–88. The data are plotted in Figure 2.*

Year	4-day periods, *n*	Total young	Slope × 100	*P*
1983	4	117	−1.8	0.69
1984	6	236	−3.0	0.06
1985	4	147	+1.6	0.12
1986	5	239	−6.7	0.04
1987	6	228	−1.4	0.40
1988	5	271	−3.4	0.01

trend was not quite statistically significant ($P=0.06$). No seasonal effect was apparent in the other three years (Fig. 2, Table 2). Over the 20-day hatching period the proportion of chicks surviving declined on average from 56% to 27% in 1986 and from 33% to 24% in 1988.

Growth rates

There were significant annual differences in the slopes of the regression of weight against wing-length (ANCOVA $F_{5,1246}=3.36$, $P<0.005$). Pairwise comparisons showed that chicks in 1983 had a significantly lower average growth rate than those in 1984, 1985 and 1986, while those in 1986 grew faster than chicks in 1985 and 1987 and those in 1988 faster than those in 1987 (*F*-values, all $P<0.05$).

Plots of weight against wing-length for survivors and non-survivors in a year showing a seasonal decline in survival prospects with date (1988) and a year with no seasonal trend (1985) are presented in Figure 1. In none of the years was there a significant difference in either the slope (ANCOVA *F*-values, $P=0.15$–0.72) or the intercept (ANCOVA *F*-values, $P=0.20$–0.83) of the regression lines for survivors and non-survivors. Survival of the 10% of chicks with the highest and lowest condition indices in any year did not differ significantly from the average annual survival rate (all Fisher's exact tests, n.s.). In 1984 and 1987 (but not in the other years) there was a significant decline in the condition index with hatching date but in both cases the date of hatching explained less than 3% of a bird's condition ($r=-0.16$, $n=241$; $r=-0.17$, $n=227$). In the other years (including the two where that was a seasonal decline in post-fledging survival) no such decline was evident.

DISCUSSION

Searches for ringed Guillemots on the Isle of May were as intensive as possible, but nevertheless some birds which returned will undoubtedly have been missed and others which survived may have recruited into other colonies. Such birds will be included in the non-survivor category and will dilute any observed effect of weight or hatching data on survival. We cannot quantify this dilution but the percentages of young recorded as survivors are similar to those reported for the survival of young to breeding age (Hudson 1985), which suggests that we saw a high proportion of the surviving young.

Our finding of a significant seasonal decline in post-fledging survival in two years appears to be the first time that this has been demonstrated in the Alcidae. There is much evidence that young Guillemots suffer heavy mortality in the first autumn (Birkhead 1974, Bayer *et al.* 1991) and Ydenburg (1989) stressed the need for early fledging so that a chick could grow as much as possible before the onset of winter. The difficulties involved in obtaining survival data of this type often result in small numbers of 'survivors' being recorded so that data have to be pooled across years (Hedgren 1981, Lloyd 1979), whereby any differences between years could be masked. In every year on the Isle of May there was a significant decline in breeding success (measured up to the time that the chick left the colony) through the season (Wanless & Harris 1988, updated). Thus there is an advantage to a pair in breeding as early in the season as possible. In years such as 1986 and 1988 there was the additional advantage such that a pair breeding at the start of the season had overall a two- to three-fold greater chance of having a chick survive to return to the colony than did a pair laying 3 weeks later.

1986 and 1988 were obviously good years for Guillemots on the Isle of May, when the growth of chicks, breeding success and post-fledging survival were all above average for the colony (this study, unpubl. data). It is therefore tempting to assume that seasonal declines in postfledging survival are associated with good breeding years, perhaps because success of early young is enhanced, but more data are needed to test this hypothesis.

Despite the suggestion that chicks grew particularly well in years when subsequent survival was high, in none of the years did the growth rate of chicks which survived differ from that of chicks which did not. A similar result, using fledging weight, was obtained in the Baltic during 6 breeding seasons (Hedgren 1981). Guillemot chicks are only one-quarter to one-third grown when they leave the colony with the male parent; young from the Isle of May do not reach adult weight until 6–8 weeks later (Harris, Webb & Tasker 1991). Growth after leaving the colony, or weight at independence which is assumed to occur about this time, might influence a chick's survival prospects but there seems little hope of collecting data to test this.

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